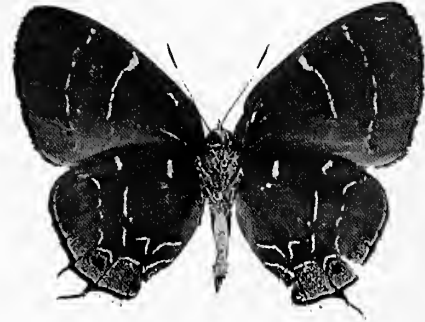


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## The life history of *Hypanartia dione dione* (Lepidoptera: Nymphalidae) in northeastern Ecuador.

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**Abstract.** Little has been published on the natural history of the strictly Neotropical nymphalid genus *Hypanartia*. We describe, for the first time, the early stages of *Hypanartia dione dione* from rearings in eastern Ecuador. Plants from two genera, *Cecropia* (Cecropiaceae) and *Boehmeria* (Urticaceae), are used as larval food plants. Larvae construct and inhabit shelters on the food plant leaves which are similar in many respects to those built by some members of the family Hesperiiidae. Larval coloration and general morphology are similar to *H. d. arcaei* from Costa Rica.

**Key words:** Andes, cloud forest, food plant, larva, pupa, shelter.

### INTRODUCTION

The genus *Hypanartia* Hübner 1821 includes 14 species of nymphalid butterflies, all with orange, brown, or reddish ground colors to their angular and tailed wings. They are distributed throughout Central and South America, with the equatorial Andes as their center of diversity (Willmott *et al.*, 2001). The natural history of most species is poorly known, with published larval descriptions available for only four species (DeVries, 1987; Toledo, 1973; Wolcott, 1924; Young 1976). From these we know that the genus feeds predominantly on Urticaceae and Ulmaceae, with one record from Cuba of *H. paullus* (Fabricius, 1793) feeding on *Piper* (Piperaceae) (Alayo & Hernandez, 1987).

*Hypanartia dione dione* (Latreille, 1813) (Fig. 1) is one of three subspecies and is distributed throughout the Andes on both slopes from Venezuela to Ecuador and along the eastern slopes south to Argentina (Willmott *et al.*, 2001). Apart from photographs in Janzen and Hallwachs (2005), nothing has been published concerning the early stages of this species. Here we describe the larva, pupa, larval shelter building behavior, and host associations of *H. dione dione* from northeastern Ecuador.

### MATERIALS AND METHODS

We made all collections in the vicinity of the Yanayacu Biological Station and Center for Creative Studies (YBS, 00°35.949 S, 77°53.403, 2100 m), located

5 km west of the town of Cosanga, Napo Province, eastern Ecuador. We collected larvae from the adjacent Hacienda San Isidro private reserve owned by the Bustamante family and along the Huacamayos ridge, 5 km to the south. On 6 November 2001, we collected one first and one second instar along a small stream in the San Isidro preserve at an elevation of approximately 2050 m. Additionally, we collected two egg shells from the bottom surface of the leaf. Subsequently, on 22 November, we collected one fourth instar, nine fifth instars, and two sixth instars at an elevation of approximately 2300 m along the Huacamayos ridge. We returned all larvae to YBS and reared them inside glass jars by providing fresh leaves every two days. In total, we reared six to eclosion. We made larval length measurements at the time of premolt or prepupa, when feeding had stopped. To avoid artifacts of enclosure, we only included observations of shelter building behavior and construction that were made in the field at the time of collection. We preserved one fifth instar, one sixth instar, and one pupa in 70% alcohol after dropping them into boiling water as described by DeVries (1987). Subsequently, we reared numerous individuals from three different host plants. All early stages and adult vouchers are retained in the first author's personal collection.

### RESULTS

*Cecropia litoralis* (Cecropiaceae), *Boehmeria caudata*, and *B. ulmifolia* (Urticaceae) are used as larval food plants by *Hypanartia d. dione* in our area. All instars rested in leaf shelters constructed by the larva. We never encountered frass inside shelters, yet larvae did not forcibly eject frass as described for shelter building

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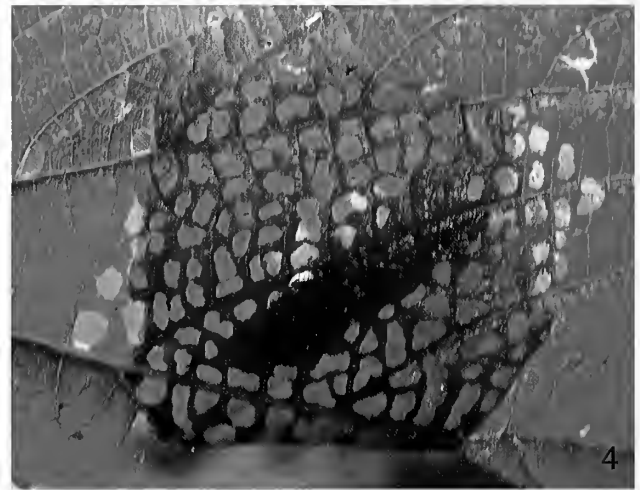
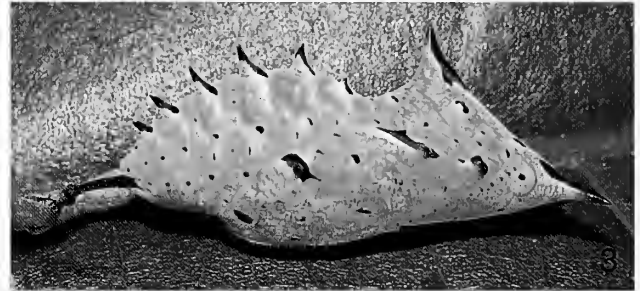
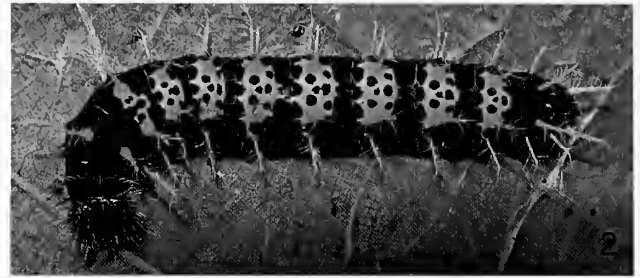


**Figure 1.** Adult *Hypanartia d. dione* puddling at urine enriched soil, Yanayacu Biological Station, Napo, Ecuador, 2100 m. Photo by H. F. Greeney.

Hesperiidae (Scoble, 1992; Weiss, 2003). As little has been written on nymphalid larval shelters, discussions and descriptions follow those outlined for hesperiids (Greeney & Jones, 2003).

**Egg.** (n=2 hatched shells, 0.9 mm wide). Round to slightly elongate with 11 strong vertical ridges. Eggs were found singly, on the ventral side of mature leaves, both on small *Cecropia sp.* saplings in disturbed areas.

**Larva.** First instar (n=1, to 3 mm). Head round to roundly square, dark red-brown with sparse dark setae varying in length from minute to short; body roughly round in cross section, entirely clear yellow-orange including prolegs, with darker viscera showing through along midline after the onset of feeding, true legs black; prothoracic shield similar to that described for second instar, T1 with long dark forward-projecting setae and with subspiracular small fleshy lump tipped with several short dark setae; T2 and T3 with small fleshy lumps subdorsally, slightly lower than those on abdomen, slightly larger fleshy lumps spiracularly and smaller lumps subspiracularly as described for T1, all lumps tipped with sparse short dark setae; A1 to A8 with lumps as described for thorax, one subdorsal, one supraspiracular, and one subspiracular, supraspiracular



**Figures 2 - 4.** Early stages of *Hypanartia d. dione* at the Yanayacu Biological Station, Napo, Ecuador, 2100 m. Photos by H. F. Greeney. 2. Fifth instar. 3. Pupa. 4. Leaf shelter of final instar.

lumps slightly anterior of others, subdorsal lumps on A8 slightly larger than other abdominal lumps and similar in size to subdorsal lumps on T2 and T3; A9 and A10 with lumps supraspiracularly only, anal plate unsclerotized and with sparse fringe of short pale setae. Second instar (n=1, to 8 mm). Head as described for first instar but shining black; body similar in shape to first instar but now orange-green; prothoracic shield shining black, narrow, dorsal only, T1 setae and fleshy lump as described for first instar, several setae arising from prothoracic shield; T2 to A10 as described for first instar, fleshy lumps replaced by short black conical scoli, scoli with short sparse dark setae and tipped

with a single long black seta; A9 with small mid dorsal roughly round sclerotized patch with short dark setae, fringe of setae on anal plate pale orange. Third instar (n=2, to 13 mm). Head and body as described for second instars but dorsum of T3 to A7 with irregular bright white frosting, white markings reducing orange-green color to small spots, all scoli as described for second instar but slightly longer and setae near apex paler, shining black sclerotized patch on mid dorsum of A9 now more distinct, anal plate weakly sclerotized, clear. Fourth instar (n=4, to 18 mm). Head and body as described for third instar, white dorsal pattern now extending slightly onto T2 and A8 as stripes on either side of midline, most of larger setae on body and scoli now pale, prolegs with sclerotized shining black plates laterally. Fifth instar (n=11, to 26 mm, Fig. 2). Head as described for fourth instar but now epicranial suture more depressed giving an overall slightly heart shape; body now all velvety black dorsally and laterally, venter dark purple black and all parts of the exoskeleton are the same when stretched (e.g., on T1 during premolt), dorsal bright white pattern very prominent, more defined and not extending onto T2 and A8, becoming pale yellow to bone colored late in instar; T1 still with subspiracular fleshy lump, all scoli prominent and elongate, scoli on T2 (all), T3 (spiracular), A8 (sub and supraspiracular), and A10 (all) tipped clear to pale yellow, remaining scoli entirely clear to pale yellow, color of scoli slightly variable with some individuals having black bases on all scoli and lacking pale tipped scoli altogether. Sixth instar (n=13, to 40 mm). As described for fifth instar. Dorsal markings now bright yellow, broken into rectangles with large black spots, intersegmentally with thin black lines, pattern on T3 now reduced to thin broken line with yellow around base of subdorsal scoli.

**Pupa** (Fig. 3). Robust, widest at thorax, tapering slightly near head; bright green with scattered black flecking and with prominent, robust black spines, each with dark red markings; 12 spines form a double row along dorsal abdomen, an additional three project laterally from either side, one from the abdomen at posterior margin of wing pads and two from the thorax along the dorsal wingpad margin; thorax produced dorsally into a large spine and two forward-projecting spines adorn the head; cremaster black with variable amount of green, especially dorsally; pupal silk pale brown.

**Larval shelters.** From abandoned and inhabited shelters found in the field at the time of collection, it appears that larvae make at least three separate shelters during their lifetime. Observations suggest that first instars build an initial shelter and remain there for molts to second and third instars. Third

instars build a second shelter part way through the stadia and remain in this shelter for molting to fourth and possibly fifth instar. Sometime late in the fourth or during the fifth instar, larvae build a third shelter and then possibly a fourth. All larvae rest upside down on the ventral surface of the leaf. First shelter (n=2, roughly 10 mm by 10 mm). Following Greeney and Jones (2003), first shelters would be termed "two-cut unstemmed folds." Two major cuts are made from the leaf margin, beginning roughly 10 mm apart and approaching each other at the distal ends only slightly. The cut away section or "lid" is then folded under the leaf along a broad "bridge" and sealed tightly with silk to the ventral surface of the leaf. This forms a roughly square pocket. Feeding during the first, second, and early third instar results in small perforations in the leaf around the shelter and a few on the lid and floor of the shelter. Second shelter (n=4, roughly 15 mm by 35 mm). Second shelters are as described for first shelters, with the two major cuts originating approximately 35 mm apart along the leaf margin and approaching each other at the distal ends only slightly. These also would be termed "two-cut unstemmed folds" (Greeney & Jones, 2003). Once again the shelter lid is folded to the ventral surface of the leaf and tightly silked. Feeding damage creates many large perforations in both the lid and floor of the shelter. Only a narrow section across the middle of the shelter is left unperforated. The larvae rest along this section. Third shelters (n=9, roughly 45 mm by 60 mm, Fig. 4). As described for second shelters, with numerous, relatively smaller perforations. Fourth shelter (n=1 or 2, roughly 70 mm by 115 mm). It is uncertain if the two large shelters observed were in addition to the third shelter. The larger size and presence of empty shelters found nearby (matching the description of third shelters) suggest these are fourth shelters. Both were as described for third shelters.

## DISCUSSION

The early stages described here closely match the photographs displayed for *H. dione arcaei* from Costa Rica (Janzen & Hallwachs, 2005). In that database, 13 rearing records are given, 11 on *Urera* spp. (Urticaceae) and 2 on *Cecropia polyphlebia* (Cecropiaceae). These, along with our records reported here, appear to be the first published indication that *Hypanartia* uses hosts in the family Cecropiaceae. The similarities between the caterpillars of *H. d. arcaei* and *H. d. dione* suggest that they may be correctly included within the same species as suggested by Willmott *et al.* (2001).

While we have long known that *Hypanartia* caterpillars construct and rest in shelters built on the

food plant leaf, this is the first study to describe the shelters in detail. The similarities in construction and morphology seen between the shelters of *H. d. dione* and some Hesperiidae (Greeney & Jones, 2003) suggest that specific details of shelter architecture may have important ecological implications. In fact, even some of the secondary modifications to the basic shelter plan, most notably the chewing of many small holes or perforations in the shelter walls, is also a characteristic of the shelters of some hesperiids (Greeney & Jones, 2003; Young, 1991). While many functions have been proposed for shelter building by larval lepidopterans (e.g. Damman, 1987; Henson, 1958; Loeffler, 1996; Sagers, 1992; Sandberg & Berenbaum, 1989), we still understand little about the relationship between function and shelter architecture. As evidenced by the diversity of lepidopterans which build larval shelters (DeVries, 1987, 1997; Greeney & Jones, 2003; Scoble, 1992; Stehr, 1987), these retreats surely serve important functions. Undoubtedly we still lack the details and taxonomic understanding of specific shelter-building behaviors, and we suggest that future studies pay more attention to the details of this interesting and widespread behavior.

## ACKNOWLEDGEMENTS

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## Updated phylogeny, taxonomy, and diversification of *Janthecla* Robbins & Venables (Lycaenidae: Theclinae: Eumaeini)

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**Abstract.** The phylogeny of *Janthecla* is updated using new information on outgroups and adding two newly described species from the Upper Amazon Basin. Evidence that *Allosmaitia* and *Laothus* are the closest relatives of *Janthecla* is outlined. *Janthecla adrienne* Robbins n. sp. is described from wet lowland rain forest in Peru, and *Janthecla halli* Busby & Robbins n. sp. is named from rain forest in Ecuador. Topology of the updated cladogram is essentially the same as in the original analysis, but a new synapomorphy for *Janthecla* is identified. *Janthecla adrienne* is sister to the remainder of *Janthecla* except for *J. rocena*. *Janthecla halli* belongs to the nine-species *J. sista* clade, which is not well resolved phylogenetically. *Janthecla adrienne* has upturned frons scales, a trait that is otherwise shared in the Eumaeini only with some species of *Laothus* and *Evenus*. The relatively rapid diversification within the *J. sista* clade is discussed.

**Key words:** butterflies, frons, hairstreaks, Lepidoptera, Neotropics.

### INTRODUCTION

*Janthecla* Robbins & Venables (Lycaenidae: Theclinae) is a ten-species Neotropical eumaeine genus that primarily inhabits wet lowland forest (Robbins & Venables, 1991). Although most species have a similar ventral wing pattern, the only identified synapomorphy was a structural detail of the female genitalia (Robbins & Venables, 1991). *Janthecla rocena* (Hewitson) ranges from Mexico to southern Brazil, but eight lowland and one cloud forest species have more restricted distributions. The outgroup for a 1991 phylogenetic analysis based on adult morphological characters was "all other eumaeines" because close relatives of *Janthecla* were unknown (Robbins & Venables, 1991). The analysis resulted in few well resolved nodes (Robbins & Venables, 1991).

New information provides the opportunity to update and expand this analysis. *Janthecla* was recently placed in the *Allosmaitia* Section of the Eumaeini along with *Allosmaitia* Clench and *Laothus* K. Johnson, Kruse & Kroenlein (Robbins, 2004b). Also, two new species of *Janthecla* have been discovered in the Peruvian and Ecuadorian Amazon (Robbins, 2004b).

It is the purpose of this paper to infer phylogenetic

relationships among *Janthecla* species (including the newly described ones) using *Allosmaitia* and *Laothus* as outgroups, to describe the two new species, to discuss new character evidence from these species relating to the *Allosmaitia* Section, and to use this updated information to examine diversification within *Janthecla*.

### MATERIALS AND METHODS

In addition to collections seen previously (Robbins & Venables, 1991), new data were recorded from *Janthecla* specimens in Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru (MUSM), Universidade Federal do Paraná, Curitiba, Paraná, Brazil (DZUP), Museo Ecuatoriano de Ciencias Naturales (MECN), Quito, Ecuador, National Museum of Natural History, Washington, DC, USA (USNM), Oregon State University (OSU) and the private collections of Robert C. Busby (RCB), and Jason Hall and Keith Willmott (JHKW).

Standard entomological techniques were used (Robbins & Venables, 1991). Genitalic terms follow those in Klots (1970), as illustrated in Robbins (1991), and wing vein terminology follows Robbins and Venables (1991). Forewing lengths were measured with a vernier caliper and reported statistically as a mean and standard deviation (SD) with sample size (N). The data

**Table 1.** Character matrix (14 taxa, 13 characters) for *Janthecla* including outgroups *A. coelebs* and *L. barajo*. The characters were modified slightly from Robbins and Venables (1991).

Taxa	#1	2	3	4	5	6	7	8	9	10	11	12	13
<i>A. coelebs</i>	0	0	2	1	1	0	1	2	3	?	0	0	1
<i>L. barajo</i>	0	0	2	1	0	2	1	0	0	?	0	0	1
<i>J. rocena</i>	1	1	2	0	0	0	1	0	0	?	1	0	0
<i>J. adrienne</i>	0	0	2	1	0	0	1	0	0	?	1	1	0
<i>J. malvina</i>	0	0	2	1	1	1	1	1	1	?	1	1	0
<i>J. janthodina</i>	0	0	3	1	1	1	0	0	2	0	1	1	0
<i>J. cydonia</i>	0	0	3	1	1	1	0	0	2	1	1	1	0
<i>J. lea</i>	0	0	3	1	1	1	0	0	2	1	1	1	0
<i>J. armilla</i>	0	0	1	1	1	1	0	0	2	1	1	1	0
<i>J. janthina</i>	0	0	3	1	1	1	0	0	2	1	1	1	0
<i>J. sista</i>	0	0	2	1	1	1	0	0	2	1	1	1	0
<i>J. aurora</i>	0	0	1	1	1	1	0	0	2	2	?	?	0
<i>J. halli</i>	0	0	3	1	1	1	0	0	2	1	?	1	0
<i>J. flosculus</i>	0	0	0	1	1	1	0	0	2	2	1	1	0

**CHARACTERS.** 1. Length of male foreleg femur (0) shorter than length of tibia plus tarsus, (1) longer than length of tibia plus tarsus. 2. Male foreleg femur (0) without a scale brush, (1) with a scale brush. 3. Ratio of length of 2A divided by length from base of vein 2A to the forewing apex (0) >0.827, (1) >0.803 & <0.827, (2) >0.803 & <0.760, (3) <0.760. 4. Base of ventral hindwing (0) with a red spot, (1) with no red scales. 5. Ventral forewing (0) with androconial patch, (1) without androconial patch. 6. Ventro-lateral edge of tegumen (0) without processes, (1) with processes dorsal of valvae, (2) with process ventral of valvae. 7. Elbow of gnathos (0) with a keel-shaped ridge, (1) without a keel-shaped ridge. 8. Setae on valva (0) extend continuously to valva tip, (1) on valva tip & middle, but not in-between, (2) none at valva tip. 9. Ventral cornutus (0) absent, (1) arrowhead shaped, (2) "tongue-depressor" shaped, (3) slender. 10. Average width of the ventral "tongue depressor" shaped cornutus (0) <0.06 mm, (1) 0.06–0.16 mm, (2) >0.16 mm. 11. Ventral attachment of corpus bursae to ductus bursae (0) directly ventral of dorsal attachment, (1) > 0.25 mm more posterior than dorsal attachment. 12. Anterior lamella postvaginalis (0) without dorsal and ventral longitudinal striations, (1) with dorsal and ventral longitudinal striations. 13. Ventral hindwing anal angle (0) iridescent turquoise scales from vein  $Cu_1$  to the inner margin, (1) without iridescent turquoise scales from  $Cu_1$  to inner margin.

for types are given as they appear on data labels.

The character matrix with a list of the characters and their states are presented in Table 1. The ingroup species are *Janthecla rocena*, *J. adrienne* Robbins, *J. malvina* (Hewitson), *J. janthodonia* (Dyar), *J. cydonia* (H. H. Druce), *J. lea* Venables & Robbins, *J. armilla* (H. H. Druce), *J. halli* Busby & Robbins, *J. janthina* (Hewitson), *J. sista* (Hewitson), *J. aurora* (H. H. Druce), and *J. flosculus* (H. H. Druce). The outgroup species are *Allosmaitia coelebs* (Herrich-Schäffer) and *Laothus barajo* (Reakirt), the type species of *Allosmaitia* and *Laothus* respectively (Table 1). The characters from the previous matrix (Robbins & Venables, 1991) were the basis of the current analysis. To accommodate character states occurring in the new species or in the outgroups, a few were modified slightly, and one new one was added (character 13). Quantitative multi-state characters 3 and 10 had been analyzed additively (ordered) (Robbins & Venables, 1991), but were analyzed both additively and non-additively

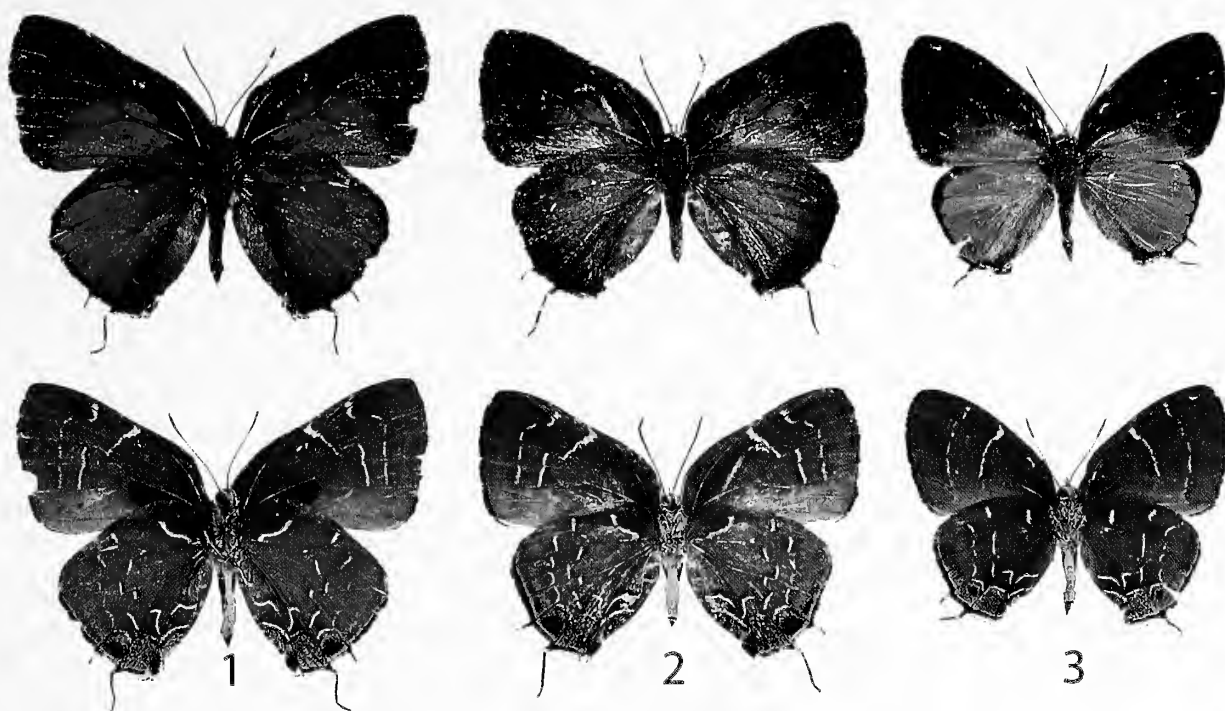
in this paper.

The implicit enumeration (ie\*) option in Hennig86 software, which searches exhaustively for shortest trees, was used to analyze the character matrix, and a strict consensus tree of all most parsimonious trees was derived. To test the assumption of equally weighted characters, a successive weighting iteration was performed (Farris, 1969). Trees were imported into WinClada software (Nixon, 2002), where character state changes were mapped using the fast optimization option. Jackknife supports were determined in WinClada using Nona (100 replications with the mult\*10 option, memory 100 trees). Distribution of *Janthecla* species (Table 2) is taken from Robbins and Venables (1991) and from the collections listed above.

## RESULTS—NEW TAXA

The two species described below belong to the Eumaeini because they have 10 forewing veins,





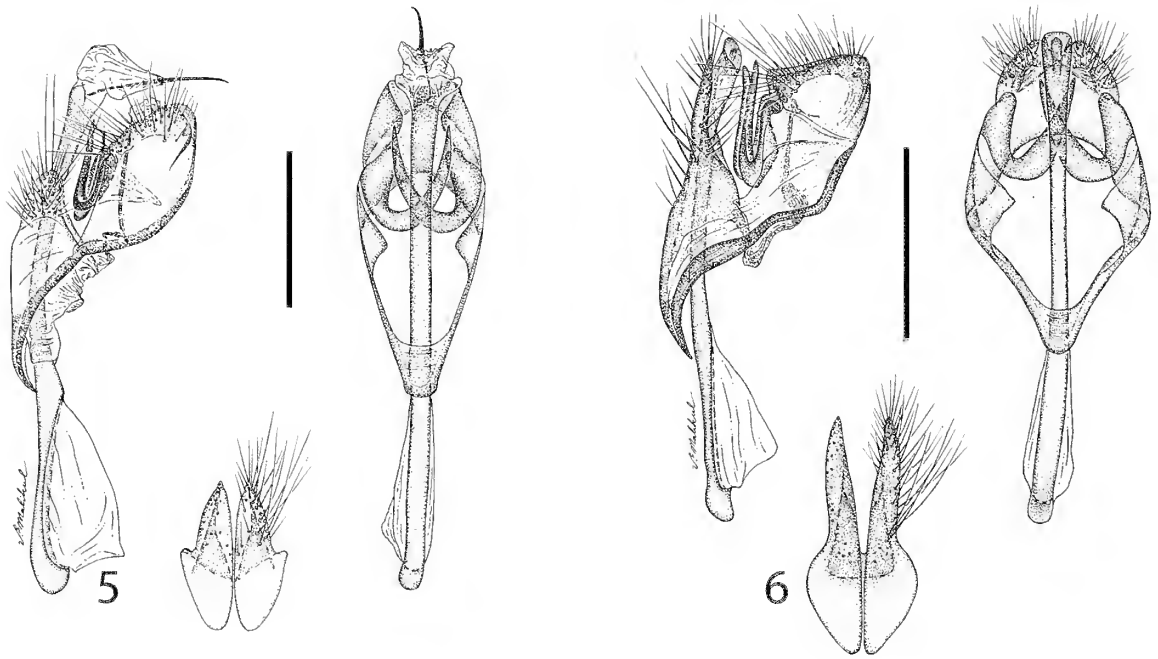
Figures 1-3. Adults of *Janthecla*, dorsal (top) and ventral wing surfaces. 1. ♂ *J. adrienne* (forewing length 16.4 mm). 2. ♀ *J. adrienne*. 3. ♂ *J. halli*.



Figure 4. Scales on frons, upturned in male *J. adrienne* (left) and downturned in male *J. halli*.

greyhound shaped male genitalia lacking a juxta, and a male foretarsus that is fused, stubby tipped, and used for walking (Eliot, 1973). *Janthecla adrienne* belongs to *Janthecla* because attachment of the female genitalia corpus bursae to the ductus bursae is more posterior ventrally than dorsally, a synapomorphy for

*Janthecla* that is unknown elsewhere in the Eumaeini (Robbins & Venables, 1991). *Janthecla halli* was placed in *Janthecla* (its female is unknown) because its ventral wing pattern and male genitalia are indistinguishable from some *Janthecla* species whose females possess the synapomorphy for *Janthecla*. It is distinguished



Figures 5-6. *Janthecla* male genitalia in lateral (left) and ventral aspects (with valvae illustrated separately for clarity). 7. *J. adrienne*. 8. *J. halli*. Scale 0.5 mm.

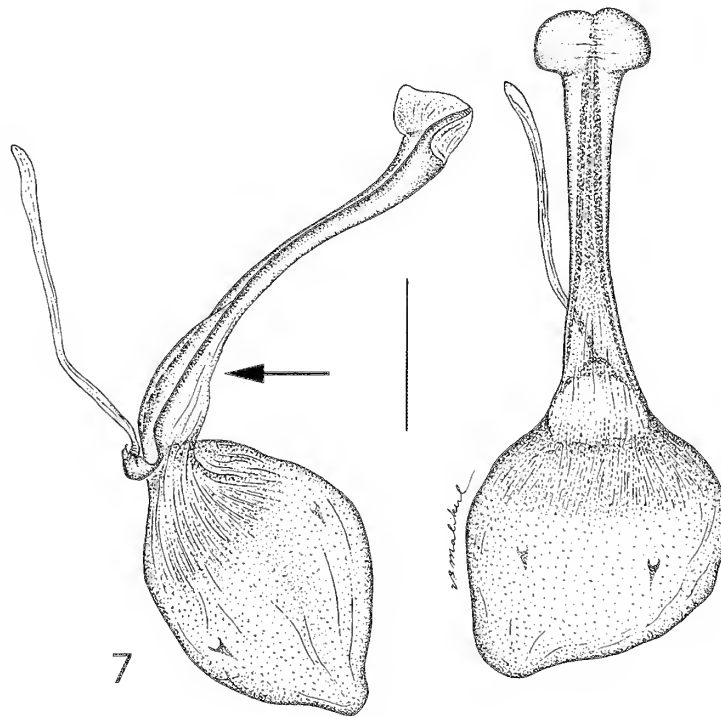


Figure 7. Female genitalia *J. adrienne* in lateral (left) and ventral aspects. Arrow points to ventral attachment of corpus bursae and ductus bursae. Scale 0.5 mm.

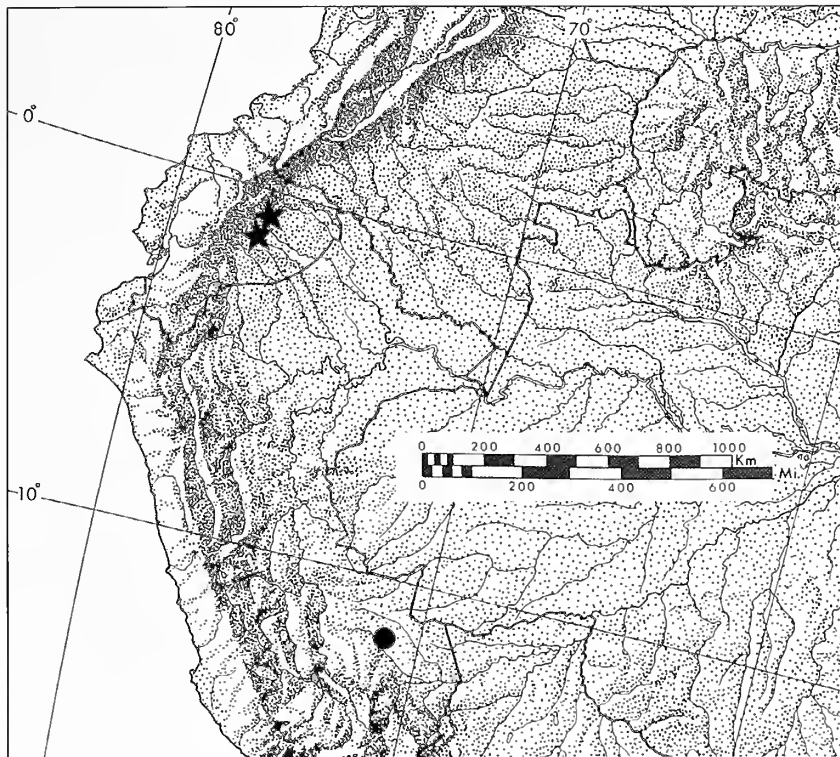


Figure 8. Distribution of *J. adrienne* (circle) and *J. halli* (star) in Peru and Ecuador.

from these species primarily by the pattern and scent patch on the dorsal forewing. Both new species share the extensive turquoise iridescent scaling at the anal angle of the ventral hindwing that is characteristic of *Janthecla*, but this scaling occurs in eumaeine genera not belonging to the *Allosmaitia* Section, most notably in *Oenomaus* Hübner and *Porthocla* Robbins.

#### *Janthecla adrienne* Robbins, n. sp.

**Diagnosis.** *Janthecla adrienne* is distinguished from all other *Janthecla* species by two characters. (1) The base of the ventral hindwing of *J. adrienne* has rust-brown scales bordered by a sinuate white line that is basally edged with black scales (Figs. 1-2). In *J. rocena*, the basal scales are red (illustrated in D'Abrera 1995: 1155). In the remaining *Janthecla* species (other than *J. adrienne* and *J. rocena*), the white line is straight and reduced in length (Fig. 3). This line is slightly curved in some individuals of *J. flocculus*, but it curves downwards towards the postmedian line, not towards the body, as in *J. adrienne* (Figs. 1-2). (2) *Janthecla adrienne* is the only *Janthecla* species with scales on the frons directed upwards, not downwards (Fig. 4).

**Identification.** In addition to the two diagnostic characters, males of *J. adrienne* are distinguished by their androconia and foreleg. *Janthecla rocena* and *J. adrienne* are the only *Janthecla* with black androconia on the ventral forewing (Fig. 1), but *J. adrienne* lacks the modification of the male foreleg of *J. rocena*, which was detailed in Robbins and Venables (1991).

**Description of Male.** *Frons* (Fig. 4). Slender brown scales

oriented upwards with a few broad white scales intermixed. Lateral edges of frons with white scales. *Antennae.* Stalk with about 18 white ringed segments. Club incrassate with about 17 segments. Yellow or orange nudum continuous on the club and as isolated patches on some segments of the stalk, as is often the case in eumaeines (Eliot 1973). *Mean forewing length* 14.4 mm, SD=0.56, N=3. *Wing Pattern.* As illustrated (Fig. 1). *Androconia* (Fig. 1). Like *J. rocena*, this species has black androconia on the ventral forewing where the hindwing overlaps it, but lacks dorsal forewing androconia. *Legs.* The foreleg is similar in morphology to that of *J. janthina*, not to that of *J. rocena*. Both foreleg structures were illustrated in Robbins and Venables (1991). *Genitalia.* As illustrated (Fig. 5).

**Description of Female.** *Frons.* Slender yellowish, light brown scales oriented upwards. Lateral edges of frons with white scales. *Antennae.* Same as male. *Mean forewing length* 14.5 mm, SD=0.45, N=2. *Wing Pattern.* As illustrated (Fig. 2). *Genitalia.* As illustrated (Fig. 7).

**Types.** *Holotype* (Fig. 1). ♂ Peru, M. de Dios, Parque Manu, Pakitza, 11°55'48"S, 71°15'18"W, 340 m, 4 Oct 1991, Leg. R. Robbins. Deposited MUSM. *Paratypes.* 1♂ same locality and collector as holotype, 11 Oct 1991 (DZUP). 1♂ Perú, M. de Dios, Parque Manu, Pakitza, 11°53'S, 70°58'W, 400 m, 12 Oct 1990 (USNM). 1♀ same locality as holotype, 14 Oct 1991, Leg. O. Mielke (USNM). 1♀ (Fig. 2) same locality and collector as holotype, 12 Oct 1991 (MUSM).

**Other Specimen.** About 13 years ago, Christian Brévignon sent Robbins a photograph of a specimen from French Guiana labeled "Saül, November 1975" from the collection of R. P. Barbotin (Cayenne). The wing pattern and androconia are nearly identical to those of *J. adrienne*. We have not been able to examine this specimen to be certain that it is the same species.

**Etymology.** This beautiful species is named for Adrienne

**Table 2.** Distribution of *Janthecla* species. "Amazon Basin" refers to areas from the Orinoco to the Amazon drainages.

<i>J. rocena</i>	Mexico to Southern Brazil
<i>J. adrienne</i>	Amazon Basin
<i>J. mahina</i>	Amazon Basin, Coastal Brazil
<i>J. sista</i>	Amazon Basin
<i>J. armilla</i>	Coastal Brazil
<i>J. aurora</i>	Coastal Brazil, Northeast Argentina
<i>J. flosculus</i>	Southern Brazil
<i>J. janthodonia</i>	Northern Central America
<i>J. cydonia</i>	Southern Central America to Western Ecuador
<i>J. janthina</i>	Central America to Western Ecuador and Northern Venezuela
<i>J. leca</i>	Amazon Basin, Western Ecuador (JHKW & RCB), Northern Venezuela
<i>J. halli</i>	Upper Amazon Basin

Venables, the co-describer of *Janthecla*. Her untimely death in 1994 was a tremendous loss for entomology. The name of this species is a noun in apposition, as Adrienne would have wanted it. It is indeclinable and non-latinized.

**Type locality.** Pakitza is a field station in Peru's Manu Biosphere Reserve that was run by the Smithsonian Institution's Biodiversity of Latin America Program in conjunction with various Peruvian academic institutions. Although the types from 1990 and 1991 have slightly different coordinates and elevations, they were collected in the same area. The data labels from 1991 are more accurate (Wilson & Sandoval, 1996).

**Habitat and Seasonality.** Pakitza is lowland primary forest. Aspects of its flora, fauna, and anthropology were detailed in Wilson and Sandoval (1996). The types were collected in October during the transition from the dry to wet seasons (when the most light reaches the forest floor) in the understory along trails through the forest. Most field work at Pakitza was done in October.

**Distribution** (Fig. 8). If the photographed specimen mentioned above is *J. adrienne*, as appears to be the case, then this species occurs over most of the vast expanse of lowland rainforest from Peru to French Guiana.

### *Janthecla halli* Busby & Robbins, n. sp.

**Diagnosis.** *Janthecla halli* is distinguished by the dorsal forewing wing pattern and by the color, placement, and size of the dorsal forewing androconial patch (Fig. 3). A broad black border covers the outer half of the forewing and the anterior wing from the costal margin to vein  $M_2$ . The triangular inner portion of the forewing is covered with brilliant blue scales and an iridescent dark green androconial patch located between the basal blue and the black border. Although the androconial patches of other *Janthecla* may reflect a greenish hue when viewed at different angles, such as the outer edge of the patch in *J. sista*, none have the androconial patch entirely iridescent dark green. The androconial patch of *J. halli* extends from vein  $M_2$  to  $Cu_2$  with at least some androconia in wing cell  $Cu_2-2A$ . The only other *Janthecla* with androconia in wing cell  $Cu_2-2A$  is *J. sista*. In worn specimens (including two of the paratypes of *J. halli*) the androconial patches have lost most of the green iridescence, but the position of the patch is essentially the same in all of the types and differs from that of all other *Janthecla*.

**Description of Male.** **Frons** (Fig. 4). A mixture of slender and broad brown scales oriented downwards. Lateral edges of frons with

white scales. **Antennae.** Stalk with about 16 white ringed segments. Club incrassate with about 14 segments. Yellow and dark orange nudum continuous on the club and as isolated patches on some segments of the stalk. **Mean forewing length.** 14.4 mm, SD=0.56, N=4. **Wing Pattern.** As illustrated (Fig. 3). **Androconia** (Fig. 3). As noted in the diagnosis. **Legs.** The foreleg femur and tibia are similar in morphology to those of *J. janthina* (illustrated in Robbins & Venables, 1991). **Genitalia.** As illustrated (Fig. 6).

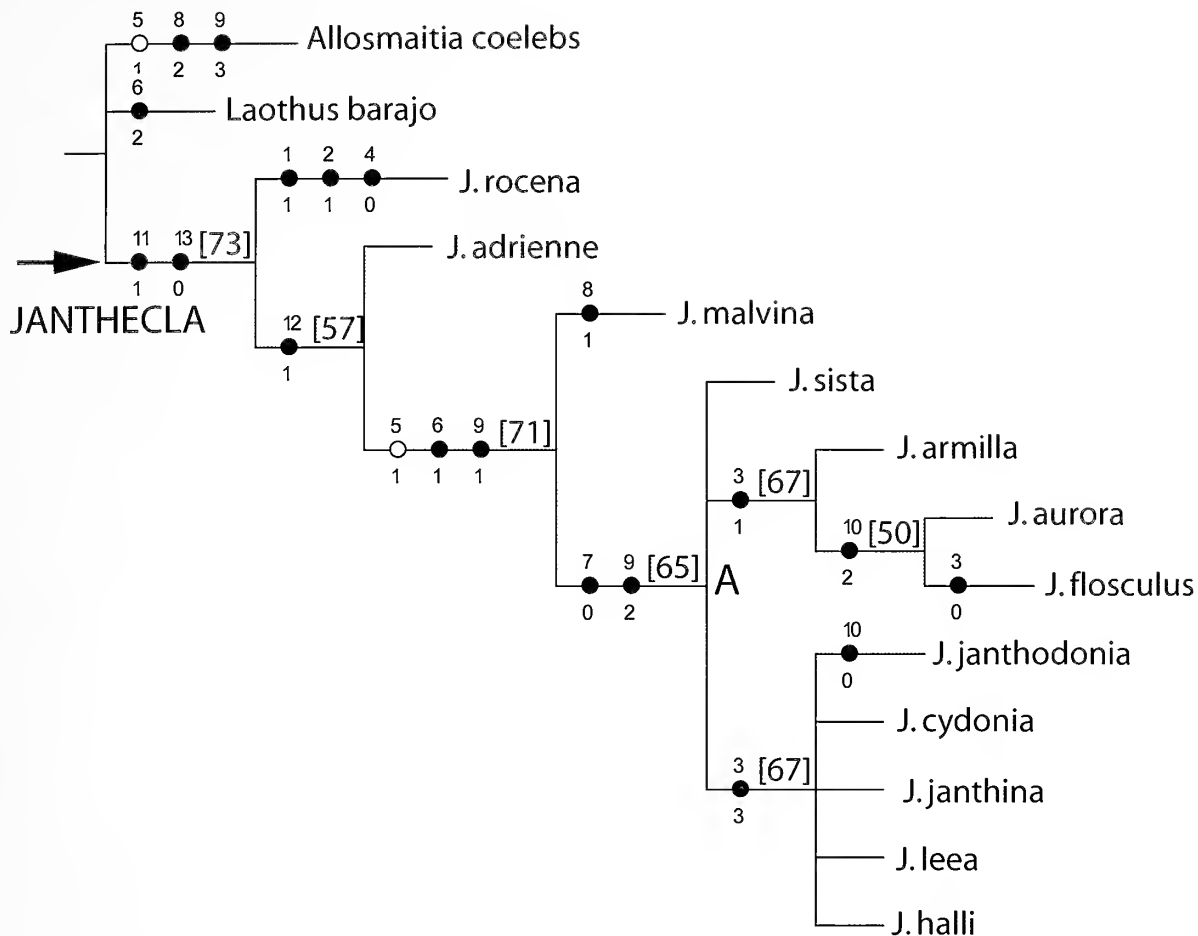
**Female.** Associating males and females of many *Janthecla* species is difficult (Robbins & Venables, 1991). Recognition of female of *J. halli* will probably require finding an adult pair *in copula*, rearing male and female siblings, or comparing DNA sequences of both sexes.

**Types.** **Holotype** (Fig. 3). 1♂ Ecuador, Napo Prov, 4 km Tena-Pano Rd., 1°02'S, 77°50'W, 600 m, 28 Sept 1990, S. S. Nicolay leg (USNM). **Paratypes.** 1♂ Ecuador, Pastaza, 10 km SW Puyo, 1°34'S, 78°02'W, 1000 m, 18 September 1990, S. S. Nicolay leg (MECN). 1♂ E. Ecuador, Napo Province, km 20 Tena-Puyo, Apuya, 600 m, 19/10/96, collected by: J. P. W. Hall & K. R. Willmott (JHKW). [Note: the Apuya locality is now at km 14, not km 20]. 1♂ Ecuador, Napo Province, 4 km W of Misahuallí, 450 m, 19-20.x.1995, leg. R. Busby (RCB). 1♂ Ecuador, Napo Province, 4 km W of Misahuallí, 450 m, 16-18.x.1991, leg. R. Busby (RCB). 1♂ Ecuador, Napo Province, Misahuallí, X-24-98, Ann Albright (OSU).

**Etymology.** This species is named for Jason P. W. Hall, who independently recognized it as a distinct species. Jason has made prodigious contributions to our knowledge of South American butterflies, especially Riodinidae.

**Type locality.** David Ahrenholz accompanied S. S. Nicolay on the trip during which the holotype was collected. He kindly provided the following description of the type locality as it was in 1990: "4 km after leaving Tena on the right side of the road was a path leading towards the Río Pano. From the road, the path cut between two fincas before dropping steeply (15 m) to a stream. The path continued beyond the stream past a school (about 600 m from the road) to the river. The area was very disturbed. A narrow band of secondary trees bordered the main road, followed by a large coffee finca, then more secondary forest down to the stream and beyond."

**Paratype localities.** The two paratypes collected by Busby were found along a shady hedgerow during the early afternoon. The hedgerow, which contained a few remnant large trees, separated an overgrown cow pasture from a finca planted with citrus trees and a few coffee plants. The hedgerow was located at least 500-1000 m



**Figure 9.** Cladogram for *Janthecla*. Characters 3 and 10 were analyzed additively. *Allosmaitia coelebs* and *Laothus barajo* are outgroups. Character numbers are placed above nodes and character state numbers below nodes. Open circles represent reversal or convergence of the character state at that node. Jackknife support is noted in brackets. When characters 3 and 10 were analyzed non-additively, this tree was one of the four shortest. Topology of a strict consensus of the four trees differs only in the collapse of the node noted by A.

from the nearest tract of "secondary" forest.

Jason Hall kindly provided the following description of the locality where the paratype from Apuya was found. "It was collected atop a broad ridge cloaked with disturbed wet rainforest. It was flying about 1 m above the ground just inside the forest edge in the early afternoon."

**Distribution (Fig. 8) and Seasonality.** *Janthecla halli* is known from 450-1,000 m elevation at the eastern base of the Ecuadorian Andes during the months of September and October.

## RESULTS—PHYLOGENETIC ANALYSIS

Addition of the new taxa and outgroups did not change the cladogram topology from the previous analysis (Robbins & Venables, 1991) except for the additional taxa. Parsimony analysis with characters 3 and 10 additive (ordered) resulted in one cladogram

with 21 steps, a consistency index of 95, and a retention index of 95 (Fig. 9). Character 5 (presence or absence of a ventral forewing androconial patch) was homoplastic, but successive weighting did not change the cladogram topology. The species from *J. janthodonia* to *J. halli* in the cladogram (Fig. 9) differ in the pattern of the dorsal forewing, including the androconia, but we were unable to code this pattern variation in a phylogenetically informative fashion. When the phylogenetic analysis was repeated with characters 3 and 10 non-additive (unordered), there were four equally parsimonious cladograms of length 21 steps, one of which was the same as the illustrated cladogram (Fig. 9). The strict consensus of these four collapses the trichotomy at node A (Fig. 9) into a nine-species bush.

## DISCUSSION

### *Janthecla* systematics

*Janthecla* had been characterized by ventral attachment of corpus bursae to ductus bursae greater than 0.25 mm more posterior than dorsal attachment (character 11), a trait that is unique within the Eumaeini (Robbins & Venables, 1991). The updated phylogeny (Fig. 9) adds a second synapomorphy; ventral hindwing anal angle with iridescent turquoise scales from vein  $Cu_1$  to the inner margin (character 13). This trait is a conspicuous wing pattern element of *Janthecla*, but its status as a synapomorphy depended on outgroup information because extensive iridescent turquoise scaling at the anal angle occurs sporadically in a variety of eumaeine genera.

*Janthecla adrienne* is a biologically and phylogenetically distinct species. Variation within the type series is small and shows no evidence of intergradation with other species. It is sympatric at its type locality with *J. rocena*, *J. malvina*, *J. sista*, and *J. lea* (Robbins *et al.* 1996). *Janthecla adrienne* is sister to the entire genus other than *J. rocena* (Fig. 9).

*Janthecla halli* is a biologically distinct species. It is sympatric with *J. rocena*, *J. malvina*, *J. sista*, and *J. lea*, but there is no evidence for intergradation with these species. There is no evidence to suggest that it is a geographical variant of the allopatric *J. janthodonia*, *J. cydonia*, or *J. janthina* (Fig. 9). For these reasons, we recognize *J. halli* as a distinct biological species even though its phylogenetic position within the genus is not fully resolved (Fig. 9).

### *Allosmaitia* section, upright frons scales, and the placement of *Evenus*.

*Janthecla* was placed in the *Allosmaitia* Section of Eumaeini with *Laothus* and *Allosmaitia* (Robbins, 2004b). Although no synapomorphy for this group has been proposed, this placement was based on similar structure of the male genitalia (*cf.* illustrations in Clench, 1964; Salazar & López, 1996) and androconia on the posterior ventral forewing in some species of each genus. With the discovery of upright frons scales in *J. adrienne* (Fig. 4), a third character common to *Janthecla* and *Laothus* has been found.

Scales on the frons are oriented downwards in the Eumaeini except for three genera in which upright frons scales occur in some species and not others. (1) *Laothus oceia* (Godman & Salvin), *L. laothoe* (Godman & Salvin), and *L. erybathis* (Hewitson) have upright oriented frons scales while *L. barajo* (Reakirt) does not (Godman & Salvin, 1887). Despite this variation, all

four were placed in *Laothus* (Robbins, 2004b) based on the proposed synapomorphy that hindwing vein  $Sc+R_1$  terminates at the middle of the costa (illustrated in Salazar & López, 1996) while it terminates at the hindwing apex in all other eumaeines (e.g., Robbins & Venables, 1991). These species also share nearly indistinguishable genitalia, similar wing patterns, and similar androconial patches. (2) As noted in this paper, all *Janthecla* species have their frons scales oriented downwards except for *J. adrienne*. (3) A third genus, *Evenus* Hübner, also has members with upright frons scales. *Evenus coronata* (Hewitson), *E. teresina* (Hewitson), and *E. leuathia* (Hewitson) have scales on the frons oriented upwards while *E. regalis* (Cramer) has them oriented downwards (Godman & Salvin, 1887). These four species were placed in *Evenus* (Robbins, 2004b) because they share a number of androconial, larval foodplant, and genitalic characters (Robbins, 2004a), especially the shape and number of the spines of the signa. However, the systematic placement of *Evenus* was problematical. While it shared the upward oriented frons scales and some androconial structures with *Laothus*, it was placed in the *Brangas* Section because of phenetic genitalic similarities (Robbins, 2004b).

Phylogenetic interpretation of the upright frons scales is ambiguous, but suggestive. The evidence in the previous paragraph indicates that the occurrence of upright frons scales is highly homoplastic, for which reason this character provides little phylogenetic information (e.g., Farris, 1969). Accordingly, *Evenus* was not placed in the *Allosmaitia* section of the Eumaeini (Robbins, 2004b). Alternately, the "tendency" for frons scales to be upright is consistent with the placement of *Laothus* and *Janthecla* in the same section and suggests that *Evenus* may also belong to the *Allosmaitia* Section. The hypothesis that this "tendency" evidence is informative will depend upon support from independent character evidence, such as DNA sequences.

### Diversification

During the time that the ancestor of the *J. sista* clade (node A on Fig. 9) diversified into nine extant species, ancestors of *J. malvina*, *J. adrienne*, and *J. rocena* did not speciate, at least as represented by known extant species. However, poor phylogenetic resolution within the *J. sista* group and unrecorded larval food plants allow only a few comments about the relatively rapid diversification within this clade. The ventral wing pattern and genitalia of all nine species of the *J. sista* group are nearly indistinguishable. Up to three species of this group may be sympatric (Table 2). Adults of these sympatric species occur in the same

habitats, oftentimes are found flying within a few meters of each other, and cannot be distinguished by their behavior. These results suggest that a “lock-and-key” mechanism (Shapiro & Porter, 1989), mate recognition of small differences in the ventral wing patterns (Fordyce *et al.*, 2002), and habitat partitioning are unlikely to have been pertinent factors in the diversification of this clade. Indeed, the only evident differences among members of the *J. sista* clade (and basically the only way to distinguish the species) are aspects of the dorsal wing pattern and dorsal forewing androconia. These dorsal wing differences are presumably related to courtship, and if so, might well be a prime factor in the relatively rapid diversification of *J. sista* and relatives.

**Postscript.** On 21 September 2006, RCB recorded more information about *J. halli*. The site was a hilltop (950 m) approximately 3 km west of Mendez, Morona Santiago Province, Ecuador. The hill was mainly cow pasture (waist-high grass) with a small remnant of secondary forest on the summit and one hillside. Late in the day, several hairstreaks were flying about each other above a small bush (2 meters high) between the forest and cow pasture on the east (shady) side of the hill. This behavior is typical of males setting up mating territories. Between 1600 and 1615 hours, three males of *J. halli* were collected, each on the top leaf of the bush they had been circling. A second visit to this site on 1 October 2006 yielded one more male on the same bush at 1615 hours. At 1625 hours, another *Janthecla* flew to the bush. It landed for two seconds, flew about seven meters, landed momentarily, returned to the original bush for a couple of seconds, landed on a smaller bush about three meters distant at the edge of the cow pasture, and was collected. It was a female. Yet another individual circled the original bush at 1655 hours, but then flew away.

The discovery of *J. halli* in Mendez represents a 135 km range extension southward but is otherwise not surprising. As with previous specimens from localities near Misahualli, Tena and Apuya, this site was disturbed and shady. While the flight time in Mendez is later in the day than the time when other individuals were collected, it is the first record of presumed territorial behavior in this species. The association of the female with the males depends upon the behavioral observations noted above. We do not yet know if this female can be distinguished morphologically from females of sympatric *J. leea* and *J. sista*.

## ACKNOWLEDGEMENTS

We gratefully acknowledge the contributions of Jason Hall and the late Adrienne Venables, as noted in the species descriptions.

Dave Ahrenholz and the late Stan Nicolay kindly contributed specimens and information. Christian Brévignon courteously sent us a photograph of the French Guiana specimen of *J. adrienne*. Vichai Malikul expertly illustrated the genitalia of the new species. For constructively commenting on the manuscript, we thank Dave Ahrenholz, John Burns, Marcelo Duarte, Brian Harris, and Gerardo Lamas. We are especially grateful to Jason Hall and Roger Vila for suggestions that substantively improved the manuscript.

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# $\delta^{15}\text{N}$ analyses of butterfly wings and bodies suggest minimal nitrogen absorption in carrion and dung puddling butterflies (Lepidoptera: Nymphalidae)

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**Abstract.** Nitrogenous compounds in the adult diet can play an important role in the nutritional ecology and life history evolution of butterflies. We compared the concentration of  $\delta^{15}\text{N}$  in fruit-feeding butterflies that feed on faeces and carrion (puddling) versus those that do not feed on these substrates, and used the difference between  $\delta^{15}\text{N}$  in bodies versus wings as a measure of the amount of nitrogen derived from animals. Differences between the sexes and between the feeding guilds were small, suggesting that minimal amounts of nitrogen were absorbed from these resources. Males, the sex that does most of the puddling, had higher  $\delta^{15}\text{N}$ , but this occurred in both carrion feeders and non carrion feeders. This probably reflects differences in metabolic activity of caterpillars. It appears that caterpillar metabolism and metamorphosis results in significant secondary  $\delta^{15}\text{N}$  enrichment and differences among the sexes, and, together with host-plant range and quality, in within species variation in  $\delta^{15}\text{N}$  values.

**Key words:** fruit-feeding, host-plant, nitrogen metabolism, sexual differences, tropical forest, Uganda

## INTRODUCTION

The commonly observed puddling behavior (feeding on mud, dung or carrion) of especially male butterflies is often interpreted as foraging for sodium (Arms *et al.*, 1974; Molleman *et al.*, 2005; Norris, 1936; Pivnick & Mcneil, 1987; Smedley & Eisner, 1995, 1996). However, carrion and faeces from predators also contain proteins and amino acids and some butterfly species show preferences for these components in the context of nectar feeding (Erhardt & Rusterholz, 1998; Mevi-Schutz & Erhardt, 2003) and puddling (Beck *et al.*, 1999; Boggs & Dau, 2004). Usage of adult diet derived nitrogen for reproduction may provide opportunities for life history evolution, including extension of life span (Dunlap-Pianka *et al.*, 1977). Males mostly puddle and males can transfer nutrients to the female in the spermatophore. Therefore, nutrients collected by the male can be used in female metabolism and reproduction (Oberhauser, 1989; Wiklund *et al.*, 1993).

$\delta^{15}\text{N}$  increases by about 3-5 ‰ per trophic level (Peterson & Fry, 1987). Butterfly wings are fully developed at eclosion and besides small amounts of

haemolymph, will thus mainly reflect the nitrogen source of larvae, whereas the bodies will reflect that of caterpillars as well as subsequent adult food. Thus, a male butterfly that fed on the remains of an insectivore in the faeces of a civet cat may be utilizing nitrogen that is 9-15 ‰ higher in  $\delta^{15}\text{N}$  than its own wings. Differences in  $\delta^{15}\text{N}$  between body and wings of an individual may thus indicate to which extent adults utilize animal derived nitrogen.

Plants vary in their  $\delta^{15}\text{N}$  depending on nitrogen sources (e.g. mycorrhiza or bacterial fixation (Hobson, 1999)). In addition, different food plants may cause different degrees of metabolic fractionation of  $\delta^{15}\text{N}$  in herbivores. Thus intra-specific variation in  $\delta^{15}\text{N}$  indicates the range of food-plants used. For example, Webb *et al.* (1998) noted that locusts fed on nutrient poor diet were enriched by 7.8 ‰ in  $\delta^{15}\text{N}$ , whereas they were only enriched by 3.1 ‰ on a nutrient rich diet. In addition, variations in butterfly  $\delta^{15}\text{N}$  content may reflect metabolic differences, especially among the sexes.

## MATERIALS AND METHODS

Butterflies were collected from fruit-baited traps at Makerere University Biological Field Station in Kibale Forest National Park, Western Uganda (0° 35'

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**Table 1.**  $\delta^{15}\text{N}$  values (‰) of bodies and wings and thorax width (mm) of fruit-feeding butterflies from Kibale National Park, Uganda

Species	Male					Female						
	thorax width	N	body mean	body range	wing mean	wing range	thorax width	N	body mean	body range	wing mean	wing range
<b>Faeces and carrion feeding:</b>												
<i>Charaxes fulvescens</i>	7.2	11	6.28	(2.52-8.15)	6.16	(2.58-8.42)	7.5	7	5.73	(2.37-8.76)	5.99	(2.51-8.65)
<i>Charaxes bipunctatus</i>	9.3	6	9.44	(6.52-10.87)	9.67	(7.04-10.93)	9.4	4	8.50	(6.92-10.18)	8.22	(7.10-9.9)
<i>Charaxes numenes</i>	8.7	2	7.07	(6.86-7.29)	7.47	(7.1-7.84)	8.6					
<i>Charaxes tiridates</i>	9.4	1	7.88		8.83		10.0	1	5.65		5.92	
<i>Harma theobene</i>	5.0	1	5.56		5.34		4.7					
<b>Not faeces and carrion feeding:</b>												
<i>Euphaedra alacris</i>	6.3	10	8.54	(6.33-9.98)	8.32	(6.54-9.41)	6.4	9	7.51	(5.73-9.03)	7.58	(6.15-9.65)
<i>Euphaedra medon</i>	5.8	10	7.02	(3.65-9.75)	7.05	(3.74-9.25)	5.7	8	7.37	(4.15-9.54)	6.56	(4.19-10.09)
<i>Euphaedra harpalyce</i>	6.5	7	5.65	(4.16-7.18)	6.16	(4.38-7.21)	6.7	3	6.16	(5.82-8.44)	7.01	(5.26-8.27)

N 30° 20' E) in July 2001. The field station borders selectively logged moist evergreen forest at an altitude of around 1500 m and is therefore classified as a transition towards montane forest. The mean maximum temperature is 23.8°C and the mean annual rainfall is 1749 mm and is bimodal in distribution (Chapman *et al.*, 2005).

The carrion feeding species included were; *Charaxes fulvescens* Aurivillius, 1891, *C. bipunctatus* Rothschild, 1894, *C. numenes* (Hewitson, 1859), *C. tiridates* (Cramer, 1777) and *Harma theobene* Doubleday 1848, the non-carrion feeding species were *Euphaedra alacris* Hecq, 1979, *E. medon* Linnaeus 1763 and *E. harpalyce* (Cramer, 1777). Specimens showing signs of wear of the wings were selected to focus on older individuals that had had opportunity to puddle. The feeding habits and thorax widths were documented using traps with rotting fish or civet dung (Molleman *et al.*, 2005). Butterflies were dried within glassine envelopes and thereafter bodies and wings were mill-ground separately. A sample from body and from wing was thereafter analyzed on the University of Cape Town mass spectrometer (Finnigan Mat 252) after combustion in an automated Carlo Erba device, using Merck gel standards.

## RESULTS

All results are summarized in Table 1. Neither male nor female bodies were  $\delta^{15}\text{N}$  enriched compared to

wings. The relationship between body and wing  $\delta^{15}\text{N}$  within individuals is both very strong and close to a slope of unity: slope for male and female non-carrion feeding wing versus body is 0.91 ( $r=0.96$ ,  $n=46$ ) and for carrion eaters it is 0.99 ( $r=0.92$ ,  $n=33$ ). Within individual differences in body and wing  $\delta^{15}\text{N}$  between the sexes and feeding guilds are small. Males may have a higher  $\delta^{15}\text{N}$  in both bodies and wings, than do females in both carrion and non-carrion feeding butterflies (e.g. for bodies Mann-Whitney U:  $p<0.20$ ,  $n=77$ ). Within each species, there was a wide range of  $\delta^{15}\text{N}$  values. Larger species may have higher  $\delta^{15}\text{N}$  values, at least among males (correlation between thorax width and average  $\delta^{15}\text{N}$  in body:  $N=8$ ,  $r=0.6$ ,  $p=0.11$ ).

## DISCUSSION

On the basis of our results it seems unlikely that the species that feed on faeces and carrion obtain significant amounts of nitrogen from this source, because the difference between wings and bodies is small in both sexes and is not different amongst the two feeding guilds. However, we did not measure  $\delta^{15}\text{N}$  of the spermatophore or eggs of carrion feeders versus non carrion feeders, and animal derived nitrogen may be incorporated into the spermatophore and thereafter transferred to the eggs. In addition, particular individuals of species that are known to feed on carrion and dung may not (or rarely) have fed on these substrates, so that little or no animal derived

nitrogen could be used in adult metabolism.

That male bodies may be enriched compared to females is not due to supplementary adult nitrogen feeding, because their wings are also relatively enriched. The differences between the sexes likely reflects sexual metabolic differences among caterpillars, as was shown by Pivnick and McNeil (1987) for the puddling butterfly *Thymelicus lineola*: male larvae consume about 85% of the foliage consumed by females, yet on adult emergence, males have a dry weight of only 48% of the females. However, at emergence males contain 82% of the total body sodium of females and the concentration is twice that in females. This suggests that caterpillars exhibit compensatory feeding for sodium. These results indicate that to understand puddling and its relationships to nutrient budgeting, an approach incorporating both larval and adult feeding will be necessary.

A surprising result was the large intra-specific variation in wing and body  $\delta^{15}\text{N}$  as a range of more than 5 ‰ occurs in several species. This would suggest broad host-plant ranges. However, for some of the species included, few host-plants have been recorded (Molleman & Hecq, 2005: *E. medon* 1, *E. alacris* 2, *E. harpalyce* 2; F. Molleman unpublished data, Larsen (1991): *C. fulvescens* 1-2, *C. bipunctatus* 1), while *C. tiridates* and *C. numenes* caterpillars have been found on a variety of plant genera (Larsen, 1991) and *Harma theobene* was found on one plant species in Kibale Forest (F. Molleman, unpublished data) but has been collected from some others elsewhere (Larsen, 1991). For the host-plant of *Charaxes fulvescens*, *Allophylus* species, we obtained a mean  $\delta^{15}\text{N}$  of 1.74 ‰ for two bulked leaf samples, considerably lower than the 8.15 ‰ maximum we obtained for this species. These results suggest that caterpillar metabolism and metamorphosis result in significant secondary  $\delta^{15}\text{N}$  enrichment.

## CONCLUSIONS

This study illustrates the usefulness of stable isotope analyses for elucidating variation in metabolism and nutritional ecology among insects. We found no evidence that adult carrion or fruit-feeding butterflies metabolize animal derived nitrogen. It appears that caterpillar metabolism and metamorphosis results in significant secondary  $\delta^{15}\text{N}$  enrichment and differences among the sexes, and, together with host-plant range and quality, in within species variation in  $\delta^{15}\text{N}$  values.

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## Cost-effectiveness of Philippine butterfly species used in live exhibits: an assessment of longevity, encounter rate and behaviour.

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**Abstract.** The importation of pupae represents a major cost for live butterfly exhibitors. Because captive butterfly species differ in life history characteristics, they should also differ in their value to exhibitors. Ten species of Philippine butterflies were imported to Wings of Paradise® Butterfly Conservatory. Butterflies were marked upon emergence as adults and were then released into the conservatory. Recaptures occurred three times daily, two to five times per week, from mid July to September, 2006. Using maximum likelihood estimation, we determined mean species longevity, encounter rate and behaviour suitability for nine of the ten butterfly species. All species demonstrated time- and age- independent survival rates. Species were found to differ significantly in longevity, encounter rate and behaviour suitability under exhibit conditions. Using the data and methodology of this study, exhibitors may select species to import based upon their relative cost-effectiveness and performance value.

**Key words:** Lepidoptera, live butterfly exhibits, life history, mark-recapture, longevity, survival rate.

### INTRODUCTION

There are over 150 live butterfly exhibits worldwide, with the majority of exhibitors stocking their greenhouses with live pupae imported from tropical breeding farms (Brewster & Otis, 2009). Exhibitors must import pupae continuously throughout the year due to the relatively short lifespan of butterflies. These pupae represent hundreds of species varying in price from US\$0.25-\$5.00 per individual (personal communication with Wings of Paradise®). Imported butterflies also vary in longevity, visibility and behaviour, affecting their usefulness in exhibits (Watts, 2004). Some species engage in crowd-pleasing behaviours such as flying, feeding, or puddling, while

others are cryptic or fly against windows, away from visitors. When importing pupae, exhibitors must balance the cost of the shipment with the appeal of the butterflies to their audience, importing both cost-effective and/or "crowd-pleasing" species.

Although there are a few existing studies documenting survival and encounter rates of butterflies in the wild (e.g. O'Brien *et al.*, 2003, survival of the pollen feeding *Heliconius charitonia*; Auckland *et al.*, 2004, survival and movement patterns of *Parnassius clodius*), there is a paucity of reliable estimates for butterfly longevity under exhibit conditions. Of the previous attempts to determine mean species lifespan in captivity (Kelson, 2002; Watts, 2004; Brewster & Otis, 2009), only Brewster and Otis implemented the appropriate mark-recapture analyses. Studies conducted by Kelson (2002) and Watts (2004) failed to control for variation in recapture success; therefore, individuals undetected during a sampling period may have been recorded as dead. Current mark-recapture methods estimate survival rate by controlling for the variation in recapture probability (the chance of recapturing an individual during a given sample

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period), thereby decreasing the likelihood that the mean survival rate would be underestimated (Altwegg *et al.*, 2003). Since the early 1990's, modeling programs such as SURVIVE, RELEASE and MARK have become popular tools for calculating population parameters using mark-recapture data (Nowicki *et al.*, 2005; O'Brien *et al.*, 2005). In this study, we estimated the survival rate of the captive butterflies using the maximum likelihood program MARK 4.2 (G.C. White, Colorado State University, Fort Collins CO).

To estimate the survival and encounter rates of a species, one must first determine whether these parameters change with time or age. Butterflies are heterothermic organisms and their activity is thought to depend on thermal conditions (Kemp, 2001). Because these environmental conditions could change daily, we predicted that butterfly encounter rate would be time-dependent. Observation at the conservatory suggests that the exhibited butterflies tend to be more active under clear skies and moderate temperatures (personal communication, Wings of Paradise®), supporting our prediction. Many individuals in the wild are thought to die from environmental risks such as diseases, predators and weather conditions; the stochastic nature of these factors may result in a survival rate that is roughly constant over time (Clements & Paterson, 1981, Speight *et al.*, 1999). In addition, a number of organisms, including some insects, have been shown to demonstrate age-dependent survival (Pollack, 1981; Harrington *et al.*, 2001; Aukland *et al.*, 2004). Nisbet and Cam (2002) argued that age dependence in survival rate reflects one of three phenomena: changes within individuals (experience and senescence with increasing age), age-

specific emigration, or mortality selection (individuals in the older age classes have lower mortality risk due to selective survival). In a controlled conservatory setting with no immigration or emigration, only the first and third phenomena could provide valid explanations if age-dependent survival was observed among exhibited butterflies. Given the favourable conditions of a conservatory, where predation is usually absent and food is abundant, we predicted that exhibited butterflies would demonstrate age-dependent survival rates.

To estimate the comparable cost-effectiveness of imported species, Brewster and Otis (2009) developed a replicable mark-recapture protocol to estimate longevity, encounter rate and behaviour for Costa Rican and Malaysian butterflies. However, the life history parameters for many other butterfly species commonly imported by exhibitors have yet to be quantified. Data on these species will help exhibitors make informed decisions during butterfly selection. The objective of this research is to determine whether ten commonly imported Philippine butterfly species differ in their longevity, encounter rate and behaviour. By quantifying these variables, we can elucidate the relative cost-effectiveness of the species in exhibit conditions.

## METHODS

Ten species of Philippine butterflies (Table 1) were imported from M. A. Corona Butterfly Culture in Marinduque, Philippines, to Wings of Paradise® Butterfly Conservatory in Cambridge, Ontario. The butterflies studied were sent in two shipments,

**Table 1.** Scientific names, common names, family names and number of marked individuals of ten Philippine butterfly species imported for a mark-recapture study at Wings of Paradise® Butterfly Conservatory. Note that *Papilio deiphobus* is sold by the distributor as *Papilio rumanzovia* and *Atrophaneura kotzebuea* is sold as *Pachliopta kotzebuea*.

Species	Common name	Family	N
<i>Atrophaneura kotzebuea</i> (Eschscholtz, 1821)	Velvet Rose	Papilionidae	16
<i>Cethosia biblis</i> (Drury, 1773)	Red Lacewing	Nymphalidae	10
<i>Danaus chrysippus</i> (Linnaeus, 1758)	Plain Tiger	Nymphalidae	21
<i>Gographium agamemnon</i> (Linnaeus, 1758)	Tailed Jay	Papilionidae	23
<i>Idea leuconoe</i> Erichson, 1834	Ricepaper	Nymphalidae	117
<i>Papilio deiphobus</i> Linnaeus, 1758	Scarlet Mormon	Papilionidae	22
<i>Papilio palinurus</i> Fabricius, 1787	Emerald Swallowtail	Papilionidae	109
<i>Papilio polytes</i> Linnaeus, 1758	Common Mormon	Papilionidae	11
<i>Parthenos sylvia</i> (Cramer, [1775])	Clipper	Nymphalidae	120
<i>Troides rhadamantus</i> (Lucas, 1835)	Troides Birdwing	Papilionidae	16

arriving 13.VII.2006 and 20.VII.2006. We marked butterflies within three hours of emergence, once their wings had dried. Using a fine-point permanent marker, each butterfly was marked with a unique three-digit identification number on the underside of each of the four wings before being released into the conservatory.

We recaptured butterflies two to five times weekly, from 17.VII.2006 to 1.IX.2006. To account for the temporal variability in butterfly behaviour, we conducted three recapture sessions on each recapture day, from 9:00-10:00, 12:00-13:00 and 15:00-16:00. Results for the three recapture sessions were pooled for the day. We recaptured butterflies with a net as we walked a consistent circuit through the conservatory. The identification number, species and the behaviour prior to capture were recorded for marked individuals. If the same butterfly was captured more than once during a session, only the first recapture and behavior was recorded.

The program MARK 4.2 (G.C White, Colorado State University, Fort Collins CO) was used to estimate the survival probabilities ( $\phi$ ) and encounter probabilities ( $p$ ) for each species using maximum likelihood estimation techniques. Survival rate is the probability that an individual will survive to the next day and encounter rate is the daily probability of recapturing an individual. The data-sets were modeled using the "recaptures only" Cormack-Jolly-Seber model (Cooch & White, 2006).

For each species, we tested seven models in MARK to determine the effects of time and age upon the survival and encounter parameters (Table 2). There are four assumptions inherent to the Cormack-Jolly-Seber model: a) all marked butterflies have the same probability of being recaptured at time ( $i$ ); b) all marked butterflies have the same probability of

surviving to time ( $i + 1$ ); c) identification markings are not lost and d) sampling is instantaneous relative to the amount of time between ( $i$ ) and ( $i + 1$ ) (White & Burnham, 1999). Assumptions c) and d) were met because all markings were made with permanent ink and the butterflies were released immediately after each recapture. Assumptions a) and b) must be satisfied by accounting for lack of fit between the model and the data (Cooch & White, 2006). The candidate models were tested and compared using Akaike's information criterion (AIC) to identify the model giving the greatest balance of model fit and estimate precision (Akaike, 1981).

Lebreton *et al.* (1992) suggested that the AIC values can be adjusted for lack of fit using the variance inflation factor,  $\hat{c}$ , a measure of extra-binomial variation. The program RELEASE (a subroutine of the program MARK 4.2) was used to calculate the variance inflation factor for each species. A  $\hat{c}$  value greater than three suggests that there is overdispersion in the data and indicates lack-of-fit for the model (Lebreton *et al.*, 1992). A  $\hat{c}$  value less than one suggests that there is underdispersion in the data, likely due to the sparseness of the data set (Boyle & Flowerdew, 1993). The variance inflation value was used to modify the AIC value to give the quasi-likelihood adjusted AIC value, QAIC. The model giving the lowest QAIC value was considered the most parsimonious and was used to estimate the values of the survival and encounter parameters for the species.

Estimates for survival probability ( $\phi$ ) and standard error were used to determine mean adult lifespan and standard error for each species using the following formulae (Leisnham *et al.*, 2003): mean lifespan =  $-\ln(\phi)-1$  and  $SE = \ln(\phi)-2 \times SE(\phi) \div (\phi)$ . Both mean lifespan and mean encounter rate were compared between species using two-tailed t-tests.

**Table 2.** Candidate models for the estimation of the survival parameter ( $\phi$ ) and encounter parameter ( $p$ ) for ten species of imported Philippine butterflies housed at Wings of Paradise® Butterfly Conservatory from July to September, 2006.

Model	Description
$\phi.p.$	Survival rate and encounter rate are both constant over time.
$\phi.p_t$	Survival rate is time dependent, encounter rate is constant over time.
$\phi_t.p$	Survival rate is constant over time, encounter rate is time dependent.
$\phi_t.p_t$	Survival rate and encounter rate are both time dependent.
$\phi_{age}p_{age}$	Survival rate and encounter rate are both age dependent.
$\phi_{age}p.$	Survival rate is age dependent, encounter rate is age independent.
$\phi.p_{age}$	Survival rate is age independent, encounter rate is age dependent.

**Table 3.** Estimates of longevity, encounter rate and behaviour suitability of ten species of Philippine butterflies housed at Wings of Paradise® Butterfly Conservatory from July to September, 2006. Standard error could not be calculated for species with time-dependent encounter rates.

Species	Longevity	±	SE (Days)	Encounter rate	±	SE	Behaviour suitability	±	SE
<i>Atrophaneura kotzebuea</i>	4.2		1.2	0.47		0.11	0.52		0.16
<i>Cethosia biblis</i>	21.5		9.9	0.19		–	1.00		0.00
<i>Danaus chrysippus</i>	10.0		2.6	0.37		–	0.68		0.12
<i>Graphium agamemnon</i>	NA		NA	NA		NA	1.00		0.00
<i>Idea leuconoe</i>	28.3		4.0	0.48		–	0.88		0.03
<i>Papilio deiphobus</i>	18.8		6.5	0.26		0.04	0.88		0.08
<i>Papilio palinurus</i>	7.8		1.1	0.20		–	0.92		0.04
<i>Papilio polytes</i>	8.9		3.7	0.47		0.09	0.75		0.19
<i>Parthenos sylvia</i>	16.0		1.9	0.29		–	0.95		0.02
<i>Troides rhadamantus</i>	13.9		5.5	0.40		0.06	0.96		0.04

**Table 4.** Comparisons between nine imported Philippine butterfly species for mean longevity and behaviour suitability. Presence of a symbol indicates a significant difference in longevity ( $\gamma$ ) or behaviour suitability (\*) between each pair of species (two-tailed t-test,  $p < 0.05$ ). Data were collected using a mark-recapture protocol at Wings of Paradise® Butterfly Conservatory from July to September, 2006. None of the species with time-independent encounter probabilities exhibited significantly different encounter rates. Encounter rates were not compared among species with time-dependent encounter probabilities.

	<i>A. kotzebuea</i>	<i>C. biblis</i>	<i>D. chrysippus</i>	<i>I. leuconoe</i>	<i>Pap. deiphobus</i>	<i>Pap. palinurus</i>	<i>Pap. polytes</i>	<i>Par. sylvia</i>
<i>A. kotzebuea</i>	-							
<i>C. biblis</i>	*	-						
<i>D. chrysippus</i>	$\gamma$	*	-					
<i>I. leuconoe</i>	$\gamma$	*	$\gamma$	-				
<i>Pap. deiphobus</i>	$\gamma$				-			
<i>Pap. palinurus</i>	$\gamma^*$	*		$\gamma$		-		
<i>Pap. polytes</i>				$\gamma$			-	
<i>Par. sylvia</i>	$\gamma^*$	*	*	$\gamma^*$		$\gamma$		-
<i>T. rhadamantus</i>	*		*	$\gamma$				

We categorized observed butterfly behaviour as either suitable or unsuitable upon each recapture depending on whether or not it enhanced the aesthetic appeal of the exhibit. Suitable behaviours included: sitting on foliage, feeding on fruit or flowers, flying, copulating, ovipositing, puddling or sitting on a visitor. Unsuitable behaviours included: flying or sitting near the windows or roof and conspicuous moribundity. For each species, we calculated the proportion of time spent performing suitable behaviours. Average behaviour suitability was calculated for each individual of a species and the mean of these individual averages was used as the behaviour suitability score for that species. Mean behaviour suitability rate was compared

between species using two-tailed t-tests.

## RESULTS

Model selection: of the ten species studied, *D. chrysippus*, *P. palinurus*, *I. leuconoe*, *P. sylvia* and *T. rhadamantus* all had a variation inflation factor within the  $1 < \hat{c} < 3$  range indicating model goodness-of-fit. *C. biblis*, *A. kotzebuea*, *P. deiphobus* and *P. polytes* all had  $\hat{c}$  values less than one, indicating underdispersion of the data. For underdispersed data, Cooch and White (2006) suggest setting these inflation variance values to  $\hat{c}=1$  for the purposes of calculating QAIC. The program RELEASE was unable to calculate the  $\hat{c}$

value for *Graphium agamemnon* due to the infrequency of encounters following their release. This resulted in data too sparse to model using program MARK. Therefore, we were unable to estimate survival or encounter parameters for *G. agamemnon* and it was subsequently omitted from our analyses.

A summary of the results on butterfly longevity, encounter rates and behaviour suitability is presented in Table 3.

**Survival probability:** the survival probabilities of all nine species were independent of both time and age.

**Longevity:** of the 36 comparisons of mean longevities among species, 11 differed significantly. (Table 4). *I. leuconoe* had a longevity of  $28.5 \pm 9.9$  days, which was significantly longer than that of six of the eight other species. *A. kotzebuea* had the shortest longevity of  $4.2 \pm 1.3$  days. This was significantly shorter than the longevities of five of the other eight species (Table 4).

**Encounter probability:** of the nine butterfly species modeled, five had encounter probabilities that varied with time (Table 3). For these five species, the probability of encounter changed daily and there was no single mean value with an associated standard error to compare among species. All five of these species had the lowest encounter probabilities on 17.VII.2006, 18.VII.2006, 2.VIII.2006 and 3.VIII.2006. The remaining four species had time- and age-independent encounter probabilities. The probability of encounter was not found to differ significantly among these four species with time-independent encounter rates.

**Behaviour Suitability Rate:** all butterfly species exhibited more suitable behaviours than non-suitable behaviours. There were significant differences in behaviour suitability rate between 11 of the 36 pairs of species (Table 4). *C. biblis* had the highest behaviour suitability rate of  $1.00 \pm 0.00$  suitable behaviours/total observed behaviours, which was significantly higher than that of five other species. *A. kotzebuea* had the lowest behaviour suitability rate of  $0.52 \pm 0.15$  suitable behaviours/total observed behaviours, significantly lower than that of four other species (Table 4). The low behaviour suitability value of *A. kotzebuea* was due to the large proportion of observation periods in which individuals of this species were seen sitting at the windows away from the public.

## DISCUSSION

Of the nine species of Philippine butterflies for which survival and encounter rates were estimated, all demonstrated significant differences in their life

history parameters and therefore, their suitability for use in live exhibits. *Idea leuconoe* had an extremely long lifespan, while *Papilio polytes* was relatively short-lived, but exhibited high behavior suitability (Table 3). The encounter data for *Graphium agamemnon* were too sparse to estimate survival and encounter parameters using program MARK. Of the 23 marked *G. agamemnon* individuals, 14 were never seen again after their initial release and the remaining nine were rarely encountered more than once. While we were unable to generate parameter estimates for this species, the extremely low encounter rate suggests that *G. agamemnon* is an inappropriate species for live exhibition.

No single species was significantly superior to all others in all three measures (longevity, encounter rate and behaviour suitability rate). Therefore, the value of the species to an exhibit depends on the relative weight given to the parameters deemed most important by the exhibitor.

The time- and age-constant survival probabilities observed for all ten Philippine species indicate that the butterflies died at a constant rate. Time- and age-independent survival is believed to be typical for many insects in the field where mortality is predominantly caused by predation and disease rather than senescence or environmental conditions (Clements & Paterson, 1981; Tsuda *et al.*, 2001). The time- and age-constant rate of survival that we observed was surprising given the generally risk-free conditions in the conservatory. Among the factors that may have influenced survival are improper larval nutrition, disease, and predation. Larval nutrition has been found to contribute to the survival of adult butterflies (Boggs & Freeman, 2005); therefore, it is possible that variable larval growth conditions at the tropical rearing farms contributed to the age-independent probability of adult survival. Diseases contracted during the larval stage may have manifested during the adult stage and this too may have contributed to the constant survival rate. Predation at Wings of Paradise®, which we initially assumed was non-existent, may have been greater than expected, resulting in mortality rates that were constant for all ages of butterflies. Possible predators were ants, frogs, spiders of several species that colonize the conservatory, or the finches and Chinese painted quail on exhibit.

Two separate shipments were pooled for the calculation of longevity, encounter rate and behaviour suitability. Ideally, the mark-recapture protocol used in this study could be repeated for each of several shipments in order to determine the consistency of the estimated parameters. Potential variability between shipments could be attributed to differences

**Table 5:** Total number of suitable days, cost per pupa and cost per day for nine species of Philippine butterflies housed at Wings of Paradise® Butterfly Conservatory from mid July to 1 September, 2006. Total number of suitable days was calculated as the product of species longevity  $\times$  average encounter rate  $\times$  behaviour suitability rate. Cost per day for a species was calculated as cost per pupa  $\div$  total number of suitable days.

Species	Total suitable days	Cost (USD)	Cost/Day (USD)
<i>Atrophaneura kotzebuea</i>	1.0	\$ 0.60	0.60
<i>Cethosia biblis</i>	4.1	\$ 0.40	0.10
<i>Danaus chrysippus</i>	2.5	\$ 0.40	0.16
<i>Idea leuconoe</i>	11.9	\$ 0.60	0.05
<i>Papilio deiphobus</i>	4.3	\$ 0.80	0.19
<i>Papilio palinurus</i>	1.4	\$ 0.80	0.57
<i>Papilio polytes</i>	3.1	\$ 0.40	0.13
<i>Parthenus sylvia</i>	4.4	\$ 0.60	0.13
<i>Troides rhadamantus</i>	5.3	\$ 0.80	0.15

in larval rearing conditions (Boggs & Freeman, 2005) or variation in shipping conditions. These pre-arrival influences can also affect the percentage of pupal losses suffered by each species. Butterflies may either arrive dead or emerge improperly due to premature eclosion during shipment, improper shipping temperature, parasitism, disease and mishandling (personal communication with Wings of Paradise®). Although it was not quantified in this study, mean species pupal loss could be used in conjunction with survival, encounter rate and behaviour suitability to provide a more comprehensive estimate of cost-effectiveness for each species.

All five species with time-dependent encounter rates had extremely low encounter probabilities on the same four sampling days (17.VII.2006, 18.VII.2006, 2.VIII.2006 and 3.VIII.2006). The first three dates were extremely hot, humid and sunny, while the last date was dark and rainy. Because butterflies are heterothermic organisms, their flight and activity are constrained by the thermal conditions (Kemp, 2001). While a minimum temperature is required for the butterflies to meet the metabolic demands of flight, Douglas (1986) suggested that in extremely hot conditions, butterflies thermoregulate by resting in shaded areas, which leads to a decrease in their encounter probability. While the environmental conditions of Wings of Paradise® are much less variable than ambient conditions, our results suggest that the temperatures and light levels in the conservatory sometimes fall outside the range suitable for activity of these Philippine species. Tighter regulation of the microclimate within the exhibit may aid in increasing the encounter probability and subsequently the cost-effectiveness of exhibited butterflies.

The butterfly species we studied did differ in life history traits. Exhibitors may use these life history values to select species which best display the desired characteristics. For example, an exhibitor may choose to import a substantial number of long-lived, highly visible species such as *I. leuconoe*. These could be supplemented with a variety of species exhibiting visitor-pleasing behaviours, such as the flower-visiting behaviour of *C. biblis*. By eliminating the importation of species with low life-history parameter values, exhibitors may either decrease importation costs or redirect funds toward increasing apparent butterfly abundance through the importation of species with higher life history parameter values. Exhibitors must also consider the overall appeal of the exhibit, a qualitative value not estimated in this study. Some visitors may appreciate high species diversity whereas others may prefer large or colourful species or large numbers of individuals.

Brewster and Otis (2009) calculated a cost-effectiveness score for exhibited Costa Rican and Malaysian butterfly species using the following formula: species cost-per-day = total suitable days  $\div$  price, where total suitable days = longevity  $\times$  encounter rate  $\times$  behaviour suitability. Using this formula, cost-effectiveness values were calculated for the nine Philippine butterfly species in this study with interesting results (Table 5). *Idea leuconoe* demonstrated the greatest number of suitable days per unit of cost, while *Atrophaneura kotzebuea* was the least cost-effective species. *Troides rhadamantus* and *Papilio deiphobus*, while among the most expensive species to purchase (\$0.80/pupa), had cost-per-day values three to five times lower than *Atrophaneura kotzebuea* pupae (\$0.60 per pupa). Note that this index does



not have an associated standard error to account for within-species variation. However, it does allow exhibitors to integrate several life-history parameters into a single value that facilitates the comparison of cost-effectiveness among species.

Conditions that improve any of these three life-history parameters for one or more species will improve the cost-effectiveness of the exhibit. The improvement and addition of fresh and/or fermented fruit, floral and sugar-rich resources may serve to increase the longevity and encounter rates of many species. For example, it is widely accepted that pollen feeding greatly enhances adult longevity and fecundity for neotropical *Heliconius species* (Boggs *et al.*, 1981; O'Brien *et al.*, 2003). Placement of feeding stations towards the interior of the conservatory may help to move individuals away from the windows. Additionally, conservatories may use either exclusion netting or specialized ventilation systems that circulate air to the centre of the greenhouse to keep butterflies away from windows. Implementation of these methods may serve to increase encounter rates and butterfly behaviour suitability. The effects of these interventions could be determined with the mark-recapture protocol employed in this study.

In summary, Philippine butterfly species differ in their longevity, encounter rate and behaviour suitability and therefore differ in their cost-effectiveness in live exhibits. The elucidation of these life history parameters enables exhibitors to make informed decisions regarding the species they import.

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# The Neo-Riparian butterfly fauna of western Argentina

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**Abstract.** In the arid and semiarid zones of western Argentina (San Juan, Mendoza and Neuquén Provinces), establishment and naturalization of exotic Salicaceae (willows and poplars) over the past 200 years has created a new type of mesic environment ("Neo-Riparian") which in turn has acquired a distinctive butterfly fauna derived from the regional species pool. These species are nearly all multivoltine and feed on naturalized exotic (weedy) host-plants. These phenomena are compared to the urban-suburban butterfly faunas of California, USA.

**Resumen.** En las zonas áridas o semiáridas del occidente argentino, en las provincias de San Juan, Mendoza y Neuquén, la introducción, cultivación y naturalización de Salicáceas exóticas (Álamos y Sauces) a partir de 1808 ha ocasionado un nuevo biotopo ("Neo-Ribereño") con una fauna correspondiente de mariposas, derivadas de la fauna regional. Son casi todas multivoltinas y utilizan plantas-hospederas naturalizadas, mayormente malezas (yuyos). Se compara estos fenómenos con sus pares en las faunas urbanas/suburbanas de mariposas californianas (EE.UU.).

**Key words:** poplars, willows, introduced species, exotic weeds, host plants.

## INTRODUCTION

Sometimes the iconic landscape of a geographic region is not "natural," but the product of human activity. Sometimes that landscape is dominated by a single species of non-native plant. For many people, Blue Gum (*Eucalyptus globulus*) is virtually synonymous with lowland California—but it has been present there for only a little more than a century (Groenendaal, 1983). For many—visitors and natives alike—Lombardy Poplar (*Populus nigra italica*) is similarly iconic of lowland Argentina, including much of Patagonia. In semiarid and arid parts of Argentina the most conspicuous trees—and often the only trees—are members of the family Salicaceae, Poplars (genus *Populus*) and Willows (genus *Salix*). But there is only one native member of the family, *Salix humboldtiana*, in the Argentine flora. All the other Poplars and Willows one sees there are introduced from the Northern Hemisphere. Some have naturalized.

Shapiro (1984) compared the Patagonian butterfly fauna with those of the arid and semiarid American West. He noted that in North America butterfly diversity is characteristically higher in riparian than in steppe or shrubsteppe habitats, while in Patagonia the reverse is true. The proximate cause of this disparity is the adaptive radiation and speciation of the Patagonian Pronophilini (Nymphalidae, Satyrinae), which are grass feeders; there is no parallel in the

North American fauna. However, this comparison only took account of the faunas associated with native vegetation and autochthonous plant communities. The present-day visitor to northern Patagonia or to irrigated valleys in the Monte, the high desert of west-central Argentina (regionally known as the Cuyo), encounters many more butterflies in riparian zones than elsewhere. This is true not only of numbers of individuals, but of taxonomic and visual diversity as well (the Pronophilines are monotonously brown): the number of species is small, but they represent a variety of lineages. This fauna as a unit appears to be of recent origin, recruited from the geographically proximate species pool. I call it the "Neo-Riparian" Fauna insofar as there does not appear to have been a significant native riparian fauna. This paper describes its ecology, makeup, and probable history. It is based on 31 years of travel and field work in Argentina, as well as on the Argentine literature.

## BACKGROUND OF THE NEO-RIPARIAN COMMUNITY

Shapiro (1991) summarizes Argentine phytogeography to that time, relying heavily on the work of Cabrera (1971). Cabrera divides the country into two Regions, only one of which, the Neotropical, concerns us here. It is subdivided into three domains. The Monte belongs to the Chaco Domain. Precipitation varies from 80-250 mm (locally higher), mean temperature from 13-17.5C, with strong E-W and N-S climatic gradients. There is year-round

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precipitation, with the heaviest falling in summer thunderstorms of monsoonal character. As usual in monsoonal climates, there is great interyear variability, and droughts and floods are both frequent. The vegetation is diverse, but dominated throughout by creosotebush (*Larrea*) and mesquite (*Prosopis*). The Monte corresponds to the Sonoran Desert of North America, to which it has been compared ecologically in great detail (Orians & Solbrig, 1977). The region is well-watered by major rivers descending from the Andes, flush with snowmelt in spring and early summer and often fed by glacial meltwater. These waters have been harnessed for both agriculture and urban use, especially for the important viticultural industry. The Payunia district in SW Mendoza Province forms an ecotone to the Western District of northern Patagonia, which Cabrera classifies in the Andean-Patagonian Domain based on floristic differences. It is a narrow fringe of shrub-steppe containing a mix of bunchgrasses and such shrubs as *Mulinum*, *Trevoa*, *Colliguaya* and *Nassauvia*. Mean annual temperature at Chos Malal in the N is 13.4°C. Precipitation ranges from 100-270 mm over the Patagonian steppe, heaviest in the W, and is more heavily frontal as one travels closer to the source of subantarctic air masses. Farther S and E is the Central District, containing the most arid part of Patagonia, from the center of the Province of Rio Negro through the province of Santa Cruz. Winters are long with frequent frost and snow, but the proximity of the ocean keeps winter minima mostly above -10°C. Summers are cool, rather cloudy and windy. Again, irrigation water is relatively abundant from Andean sources. Fruit crops and alfalfa are widely grown.

In pre-European times the extent of riparian woodland in western Argentina was very limited. The principal species were Mesquites (*Prosopis flexuosa*, *P. chilensis*) and Maitén (*Maytenus boaria*). The only native willow is *Salix humboldtiana*. The shrub *Baccharis salicifolia* and perennial herb *Pluchea* (*Tessaria*) *dodoneaeifolia* were common. Although the latter two are excellent nectar sources for butterflies, these communities do not appear to have a distinctive butterfly fauna, as riparian communities commonly do in the western United States. Species diversity is inevitably higher in the adjacent and much more extensive shrub-steppe and matorral communities, where many species of Satyrinae routinely occur. Intact examples of natural riparian vegetation are encountered mainly in the Andean foothills today; virtually all floodplain areas in the Cuyo have been transformed by human intervention.

The basic reference for historical ecology in Argentina is *Memoria Verde* by Antonio Elio Brailovsky

and Dina Foguelman (2006). This is a comprehensive historical overview of human impacts on the Argentine landscape and environment, from precolonial times to the present. With 716 footnotes, it serves as the port of entry to a rich, if little-known (outside Argentina) literature. Very briefly, Brailovsky and Foguelman tell how the agriculturalization of the country in the 19th Century led to the removal of the narrow fringe of native riparian vegetation: "Then there appeared a new factor precipitating erosion: agriculture, realized by temporary leaseholders whose interest in preserving the nearby soil was zero, and whose agronomic knowledge was initially sparse. They had to use all the land and the firewood available. Thus they cut down all the trees, including those that protected the margins of watercourses, which when the rains and floods came ended up carrying the fertility of the nearby soils far, far away." This formed part of a general pattern of wasteful agricultural practices that lasted into the 20th Century (Zarrilli, 2001). In 1886 Florentino Ameghino, an Argentine original—an autodidact-polymath best remembered as a paleontologist who developed the rich fossil beds of Patagonia and flew off on flights of patriotic fancy, declaring Patagonia the cradle of humankind—published a monograph, "Droughts and floods in the province of Buenos Aires," which is still reckoned a classic of its kind. In it he developed a detailed plan for water management, including "...the creation of artificial forests and the obligatory forestation of the margins of water courses [which] will delay erosion and permit the maintenance of the soil as a renewable resource."

Ameghino's proposals were poorly implemented systematically at a regional level, although the Immigration and Colonization Law of 1879 offered cash prizes for every 1000 trees planted on private property. Other legislation made transfer of title from the state to pioneering settlers conditional on the planting of at least 200 trees. The Mendoza Provincial Law of 1897 (Law 39) again rewarded those who planted trees, and in 1907 Mendoza institutionalized Arbor Day (Law 384). Meanwhile, construction of the national railway system had led to a demand for both ties and fuelwood that in turn led to further deforestation, mainly in the north of the country. However, the impacts were felt in the semiarid west; Ameghino wrote that in the provinces of San Juan and Mendoza "instead of augmenting them, they are destroying the few groves there had been." And flooding and alluvial deposits increased downstream in consequence. Ameghino argued that planned forestation offered multiple benefits: beyond its use in flood control, it offered shade for livestock,

recuperation of exhausted soils, and windbreaks for the protection of orchards and crops. For those who took this work seriously, the question became "What species to plant." The answer was already at hand.

The introduction of poplars in western Argentina dates from 1808 when the Spanish colonist Juan Cobo imported from Cadiz, via Chile, saplings of Lombardy Poplar and Black Poplar (*Populus nigra*) as well as other exotic trees to plant on his property in Mendoza. They thrived and grew so rapidly that they were soon propagated vegetatively and dispersed throughout the region, obviating the need to import expensive lumber for construction from Chile, Paraguay or Tucumán. The value of this introduction was so apparent that after the liberation from Spanish rule in 1810, Cobo was granted honorary Argentine citizenship for his service to the economy. This was a singular honor, since loyal Spaniards were widely discriminated against and were often the victims of harassment or violence. As early as the 1830s poplars were being used as windbreaks to shelter orchards and vineyards from both desiccation and frost. They spread to other parts of the country and were eagerly adopted, but by the 1930s disease problems in the more humid regions led to the introduction of new species, varieties and hybrids (some sterile, and only propagated vegetatively) from Italy, Germany and the United States. These eventually found their way to the Cuyo and northern Patagonia, where they "took off." Calderón (2006) writes "Here begins what can be called the second stage of poplar cultivation in our region; the new varieties grow faster and give better lumber...than our characteristic 'Creole poplars.' Still, one can yet contemplate beautiful rows of these magnificent trees in some streets of our oases..."

According to the National Poplar Commission (Comisión Nacional del Álamo, 2004) some 110,000 hectares of Argentine territory are devoted to cultivation of exotic willows and poplars. The three regions most active in the industry are the Paraná Delta north of Buenos Aires (where willows predominate) and the humid pampa of the central and northern parts of the province of Buenos Aires and the south of Santa Fe; the irrigated Cuyo in Mendoza and San Juan; and the upper valley of the Río Negro in northern Patagonia (where both genera are widely grown, but poplars are more widespread) Achinelli (2006) gives an excellent overview of the industry as it now exists.

In the Cuyo and northwestern Patagonia today, in the Provinces of San Juan, Mendoza and Neuquén, bottomlands near towns almost inevitably are planted in Salicaceae or present a vegetation dominated by naturalized Salicaceae, commonly interdigitated with small cultivated farm and garden plots and supporting

small numbers of horses, mules and other grazing domestic animals. As noted at the beginning of this article, this is today a very characteristic Argentine landscape, even though the vegetation is largely non-native. From an ecological perspective it represents a repeating community type, which has selected a distinctive butterfly fauna from the regional species pool. Butterflies are characteristically much more abundant in this "Neo-Riparian" setting than in the adjacent more-or-less natural steppe; the species mix is very different; and most of the species are today breeding on naturalized exotic host plants, which is not the case in steppe.

In addition to willows and poplars representing a number of introductions (species, varieties and hybrids), the Neo-Riparian vegetation routinely includes other exotic trees including Boxelder (*Acer negundo*), Red Mulberry (*Morus rubra*), Blue Gum (*Eucalyptus globulus* and others), Black Locust (*Robinia pseudoacacia*), Siberian Elm (*Ulmus sibirica*), and occasionally Ash species (*Fraxinus*), fruit trees, and others. The following is a partial list of plants commonly encountered in the understory of Neo-Riparian forest. The vast majority are naturalized exotic weeds, and many are of cosmopolitan distribution. Most are familiar weeds in temperate North America as well.

APIACEAE: *Conium maculatum*, *Foeniculum vulgare*.  
 ASTERACEAE: *Acroptilon (Centaurea) repens*, *Carduus nutans*, *Carduus pycnocephalus*, *Centaurea solstitialis*, *C. cyanus*, *Cichorium intybus*, *Cirsium vulgare*, *Matricaria chamomilla*, *Onopordon acanthium*.  
 BORAGINACEAE: *Echium vulgare*.  
 BRASSICACEAE: *Cardaria draba*, *Diplotaxis tenuifolia*, *Eruca sativa*, *Hirschfeldia iucana*, *Raphanus sativus*, *Sisymbrium orientale*.  
 CARYOPHYLLACEAE: *Saponaria officinalis*.  
 CHENOPODIACEAE: *Atriplex hastata*, *Atriplex patula*, *Kochia scoparia*.  
 CONVULVACEAE: *Convolvulus arvensis*.  
 FABACEAE: *Galega officinalis*, *Medicago sativa*.  
 MALVACEAE: *Malva neglecta*.  
 POACEAE: *Cynodon dactylon*.

## THE BUTTERFLY FAUNA

In addition to the species enumerated here, species from the adjacent shrubsteppe may enter Neo-Riparian areas, particularly in search of nectar. Since the reverse movement does not occur, this merely enhances the apparent diversity. All host records given here are based on direct observation of oviposition and/or larval feeding in the Neo-Riparian community since 1977. I have visited more than 30 Neo-Riparian areas in San Juan, Mendoza and Neuquén, some on

multiple occasions.

### Family PIERIDAE

*Tatochila mercedis vanvolxemii* Capronnier. (Common name "Lechera troyana")

Common; multivoltine, seasonally polyphenic. Males patrol along the edges of windbreaks and hedgerows; females found mostly in open successional fields. Populations to the east (e.g., Las Lajas, Neuquén) are apparently "pure" *vanvolxemii*, but those at the base of the Andes, such as at Barreal and Calingasta, San Juan, often show some degree of introgression from the Mediterranean Chilean subspecies *T. m. mercedis* Esch. (see Shapiro, 1991a, pp.156-166). All the known host plants in the Neo-Riparian are exotic: BRASSICACEAE: *Cardaria draba*, *Diplotaxis tenuifolia*, *Eruca sativa*, *Hirschfeldia incana*, *Lepidium perfoliatum*, *Raphanus sativus*, *Sisymbrium orientale*. The range of this entity encompasses the Monte, much of the Pampa, and the warmest parts of the eastern Patagonian steppe. In most of this region it has no native Brassicaceous hosts and may originally have been confined to Capparidaceae in the arid and subarid west; much of its current range, which extends to metropolitan Buenos Aires, may be an opportunistic response to Brassicaceous weed introductions.

*Tatochila autodice* Hubner. (Common name "Lechera común")

Common, multivoltine. This species consistently occurs in partially shaded, cooler and more humid microhabitats than the preceding, but they can be found together along roadsides and windbreaks. The southernmost populations, e.g. at Chos Malal, Neuquén, show slight phenotypic tendencies toward the Chilean-Patagonian subspecies *T. a. blanchardi* Butler, with which it intergrades in western Patagonia (Shapiro, 1986).

Again, all the known hosts here are exotic, though further south in the ecotone between the Patagonian steppe and Andean forest it breeds on native Tropaeolaceae. BRASSICACEAE: *Cardaria draba*, *Eruca sativa*, *Hirschfeldia incana*, *Raphanus sativus*.

*Colias vauthierii* Guerin. (Apparently no common name)

Common from Chos Malal and Las Lajas south, with two to three generations per year. A species of cool, moist vegas and mallines, this butterfly extends north through the province of Mendoza in the Andes but has not been found in the Neo-Riparian in Mendoza or San Juan. It is extremely abundant at Las Lajas. Females are highly variable, but always white. This

species never feeds on Alfalfa (*Medicago sativa*), though it may nectar on it. The only recorded hosts in the Neo-Riparian are FABACEAE: *Trifolium repens* (and probably other clovers).

*Colias lesbia* Fabricius. (Common name "Oruga de la alfalfa", "Isoca de la alfalfa")

Common to seasonally abundant in the north (Mendoza and San Juan) and occasional to common in the south (Neuquén), breeding on Alfalfa (*Medicago sativa*) even in the smallest patches. About half of the females are white; cold-season individuals are small, with narrowed black borders above and more or less gray shading on the hindwing beneath. At least three generations/year. This species may not overwinter in the SW portion of its range, often not being seen until the second brood in January.

### Family NYMPHALIDAE

*Auca coctei* Guerin. (Common name "Mariposa negra común")

The only Pronophilina Satyr associated consistently with Neo-Riparian habitats, this species is common in Neuquen province but has not been found in Mendoza or San Juan. At Las Lajas it is abundant in dappled light and shade and even in dense shade, preferentially visiting the yellow flowers of native *Senecio*, but also introduced weeds. It has been collected in January and February and may be univoltine. It is a grass feeder, but its host in the Neo-Riparian has not been determined.

*Vanessa carye* Hubner. (Common names "Mariposa colorada," "Dama cuatro ojos," "Dama manchada," "Pirpinto manchado")

Common throughout, with multiple generations. Males are conspicuously territorial in late afternoon, often in front of poplar windbreaks with a westerly or northwesterly exposure. Both sexes often visit the native *Baccharis* and *Pluchea* and introduced species of thistles and knapweeds. MALVACEAE: *Malva neglecta* (*M. parviflora*) and native species of *Sida*. URTICACEAE: *Urtica urens*.

*Agraulis vanillae* Linnaeus. (Common names "Mariposa de manchas plateadas," "Espejitos," "Mariposa de espejos," "Nacarada")

Common in the north (Mendoza, San Juan) and variably present in Neuquén, depending on the presence of host plants, which are cultivated and non-native in the region. Multiple-brooded, flying all year except in the coldest weather. Hosts: PASSIFLORACEAE: *Passiflora species*.



**Figure 1.** Views of Neo-Riparian habitats in western Argentina. All pictures by AMS.

**Upper left:** Lombardy Poplar windbreak in Barreal, San Juan; the arid shrubsteppe is visible at the horizon.

**Upper right:** Spontaneous vegetation of naturalized riparian trees, including Black Locust, Willow, and two species of Poplars. Drying Poison Hemlock in foreground. Arid shrubsteppe visible in distance. Las Lajas, Neuquén.

**Center left:** Orchards with Lombardy Poplar windbreak and dense population of Yellow Star Thistle in foreground. Las Lajas, Neuquén.

**Center right:** Spontaneous riparian vegetation including large Weeping Willow. Bachelor's-Button blooming in foreground. Las Lajas, Neuquén.

**Lower left:** View inside a Lombardy Poplar hybrid clone plantation, Chos Malal, Neuquén, showing mesic conditions. Across the road from this site was arid shrubsteppe with no green visible.

**Lower right:** Proliferation of weedy Brassicaceae along a farm road; *Tatochila mercedis vanvolxemii* abundant and *T. autodice* common; male *T. vanvolxemii* patrol along the edge of the poplar windbreaks. Malargüe, Mendoza.

**Family RIODINIDAE**

*Aricoris signata* Stichel. (Common name “Colage común”)

This small, inconspicuous Metalmark is common in the Neo-Riparian community in Mendoza and San Juan but has not been found in Neuquén. It visits Alfalfa flowers and sits with the wings spread. It is apparently multivoltine. The recorded host elsewhere is the native vetch *Vicia graminea*; the host in the Neo-Riparian has not been determined.

**Family HESPERIIDAE**

*Erynnis funeralis* Scudder & Burgess. (Common name “Saltarín fúnebre” or “Hesperia negra”)

Very common throughout, multivoltine. Commonly visiting Alfalfa, thistle and various Composite flowers and often entering shade. Despite numerous citations of Alfalfa as a larval host, no such relationship has been observed in the Neo-Riparian, where its sole observed host is FABACEAE: *Robinia pseudoacacia* (Shapiro, 2008). Eggs are laid mostly on coppice and sucker growth.

*Pyrgus americanus bellatrix* Plötz. (Common Name “Cuadriculada americana”)

Common and multivoltine throughout. Adults fly along linear habitats, visiting Alfalfa and numerous other flowers and also (males) mud puddles. Host: MALVACEAE: *Malva neglecta*.

*Hylephila zapala* Evans.

This little-known species is fairly common at Malargue (Mza.) and Chos Malal and Zapala (Neuquén) in association with its native host plant, the turfgrass *Distichlis spicata*. At least two, probably three broods. Visits Yellow Star Thistle (*Centaurea solstitialis*) and Alfalfa flowers. Males perch on grass or bare soil.

*Hylephila phyleus* Drury. (Common Name “Saltarín leonado,” “Saltarín dorado”—this name is also used for *Polites vibex catilina* Plötz, not in the Neo-Riparian fauna)

Abundant in Mendoza and San Juan; occasional in western Neuquén. Multivoltine. The highly territorial males perch high on roadside weeds, and both sexes eagerly visit Alfalfa, thistles and other flowers. The only host so far observed is introduced Bermuda Grass, *Cynodon dactylon*.

*Hylephila signata* Blanchard.

Common in Neo-Riparian habitat in Neuquén, but not observed further north. At least two broods. Often

visits Clover flowers (*Trifolium species*); perches on or near the ground. Host plant presumably a grass, but undetermined locally.

*Lerodea eufala* Edwards. (Common Name “Saltarín semicírculo”)

Common to occasionally abundant in the second half of the season, January through March or April, in Mendoza and San Juan; unrecorded in Neuquén. Rarely encountered in spring. Flies low and appears non-territorial; often along ditches; often found nectaring on Alfalfa with *Hylephila phyleus* and *Erynnis funeralis*. Host not determined in the Neo-Riparian.

This is a small fauna, only 14 species in total, forming a reproducible association in a well-defined anthropogenic habitat type. It is, moreover, structured geographically: *Colias vauthierii*, *Auca coctei* and *Hylephila signata* are essentially Patagonian and do not extend into Mendoza, while *Aricoris signata*, *Hylephila phyleus*, and *Lerodea eufala* are essentially northern and do not extend into Neuquén. Since all of these occurrences are in isolated floodplain or irrigated oases in the high desert and the distances among them are similar, the limitations would appear to be climatic. *Colias lesbia* and perhaps *Agraulis vanillae* show very dynamic ranges, expanding and contracting seasonally and perhaps overwintering only sporadically in areas with harsher winters, much as *Colias eurytheme* and *A. vanillae* do in the United States.

All the species except possibly *Auca coctei* are multivoltine. Of the 10 species whose Neo-Riparian host plants are known, all but one (*Hylephila zapala*) feed on non-native hosts and one (*Agraulis vanillae*) is entirely dependent on cultivated hosts. (Use of non-native hosts by native butterflies in the Southern Cone of South America has been observed at low altitudes in mid-latitudes (Shapiro, 1991a), in the high Andes (Shapiro, 2006) and in the Subantarctic (Shapiro, 1991b).) These characteristics are strikingly similar to those of the urban/suburban lowland butterfly fauna of northern California as described by Shapiro (2002) and Graves and Shapiro (2003). In fact, despite the enormous distances involved, the northern California weedy butterfly fauna shares four species with the Neo-Riparian: *Agraulis vanillae*, *Erynnis funeralis*, *Hylephila phyleus* and *Lerodea eufala*. *Vanessa carye* is the sister-species of the North American *V. annabella*; the two are extremely similar and only recently diverged (Shapiro & Geiger, 1989). *Hylephila phyleus* is the only member of its (largely Andean) genus in the Nearctic and might be introduced there. *Erynnis funeralis* is the only member of its Holarctic (mostly Nearctic) genus in South America and could also be an introduction.

As Graves and Shapiro (2003) argued, the availability of weedy hosts has probably facilitated large-scale butterfly range changes in historic time, such that species able to make use of them now occupy both areas and habitats previously closed to them.

In both lowland northern California and the Argentine Neo-Riparian community, the creation of local mesic conditions has permitted the establishment of both exotic host plants and butterflies able to exploit them. The stark contrasts between a Neo-Riparian bottomland, lush and green, and the high desert or shrubsteppe often directly across the road, underscore the impact human activity has had on the butterfly fauna of western Argentina.

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# Revisiting the pre-European butterfly fauna of the Sacramento Valley, California

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**Abstract.** The modern butterfly fauna of the Sacramento Valley, California appears poorly-adapted to the climate and native vegetation, instead reflecting drastic changes to the landscape since Europeans colonized the area ~200 years ago. This paper attempts to reconstruct the ecology of the pre-European butterfly fauna, based on current interpretations of the vegetation.

**Key words:** host plants, exotic weeds, vegetation history, butterflies.

## INTRODUCTION

The butterfly fauna of most of lowland cismontane California (west of the Sierra Nevada-Cascade axis) is very peculiar in two respects: it appears grossly mismatched with the climate in which it occurs, and it is largely dependent on non-native larval host plants (Shapiro, 2002; Graves & Shapiro, 2003). Nearly all the species making up this fauna are multivoltine, despite the fact that no rain typically falls from April through October and no native host plants are available in most habitats during that time. The adjacent foothill faunas are overwhelmingly uni- or at most bivoltine (Shapiro, 1975; Shapiro *et al.*, 2003) thus matching the seasonal availability of their native hosts. But most of the Valley fauna today breeds on naturalized exotic plants, whose availability in summer depends on water supplied by human activity. Over 30 years ago I profiled the extant Sacramento Valley fauna as then understood and attempted to place it in an historical and geographical context (Shapiro, 1974a). Our understanding of pre-American ecology in the Sacramento Valley has improved substantially since then. This paper attempts to review the probable history and sources of this fauna in that updated context.

## HISTORY OF SACRAMENTO VALLEY VEGETATION RECONSTRUCTIONS

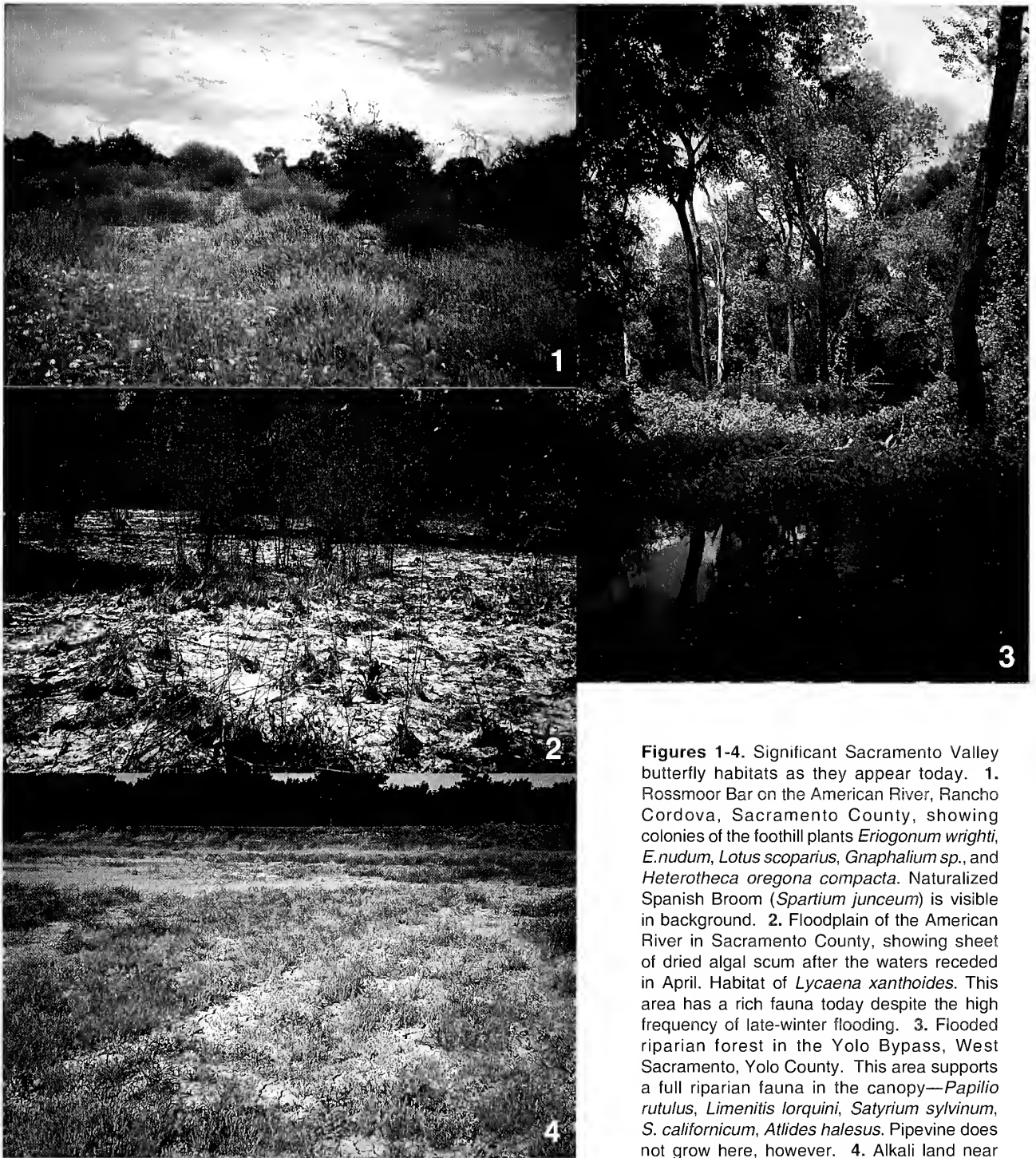
Plant ecologist Michael Barbour has said that coastal and interior [lowland] California “within 200 years experienced one of the most complete human-caused landscape transformations in the world.” While this is certainly true, there is no unanimity as

to the nature of the Sacramento Valley landscape or its vegetation before European colonization. Shapiro (1974) relied heavily on the characterizations provided by Thompson (1971), Sculley (1973) and Bakker (1971). All of these authors in turn accepted the then-conventional wisdom that much of the Valley had been a bunchgrass grassland dominated by *Nassella* (then put in *Stipa pulchra*). This was the area identified as “alluvial plains—formerly savanna” on Shapiro’s Fig. 2. Following the conventional wisdom, the accompanying text states that “Most of the bunchgrass prairie was put into pasture or under the plow; either way, the native bunchgrasses were competed out of existence by introduced annual grasses, mostly from Europe. With the bunchgrasses most of the native flora, both annual and perennial, also succumbed, to be replaced by weedy... aliens.” But was there ever such a bunchgrass prairie and if not, why was it thought to have existed?

As late as 1977, Heady was promoting the bunchgrass prairie concept, but by 1981 serious questions had emerged. Bartolome and Gemmill (1981) argued that the ecological characteristics of *N. pulchra* made it an improbable dominant species. Wester (1981) could find no contemporary documentation to support the concept in the San Joaquin Valley. Holland and Keil (1989, 1995) questioned its validity. Hamilton (1997) examined the issue and concluded that – like many erroneous notions in North American plant ecology – the bunchgrass prairie concept grew out of Clementsian dogma rather than direct observation or even indirect inference. Clements himself (1920, 1934) had interpreted persistent stands of *N. pulchra* along railroad rights-of-way as relicts of a previously dominant condition, much as relicts of tall-grass prairie persist along (unsprayed) railroad corridors in the Midwest where much of the nearby landscape was agriculturalized in the 19th Century. In addition to

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**Figures 1-4.** Significant Sacramento Valley butterfly habitats as they appear today. **1.** Rossmoor Bar on the American River, Rancho Cordova, Sacramento County, showing colonies of the foothill plants *Eriogonum wrighti*, *E. nudum*, *Lotus scoparius*, *Gnaphalium* sp., and *Heterotheca oregona compacta*. Naturalized Spanish Broom (*Spartium junceum*) is visible in background. **2.** Floodplain of the American River in Sacramento County, showing sheet of dried algal scum after the waters receded in April. Habitat of *Lycaena xanthoides*. This area has a rich fauna today despite the high frequency of late-winter flooding. **3.** Flooded riparian forest in the Yolo Bypass, West Sacramento, Yolo County. This area supports a full riparian fauna in the canopy—*Papilio rutulus*, *Limenitis lorquini*, *Satyrus sylvinus*, *S. californicum*, *Atalides halesus*. Pipevine does not grow here, however. **4.** Alkali land near Woodland, Yolo County: home of *Brephidium exile*, *Pyrgus scriptura*, *Polites sabuleti*.

the railroad corridors, the most important supposed bunchgrass relict is located at Maine Prairie Road near Dixon, Solano County, at the northern edge of the Montezuma Hills— a site which has never been

plowed. Wester (1981) noted that this site is unusual in being strongly influenced by the “sea breeze” coming through the Carquinez Strait gap in the Coast Range to the west, and thus cooler and moister than most

of the Valley, an argument reinforced by Dremann (1987) who noted that many species are “anomalously” distributed in agreement with this maritime influence. Holstein (2001) argues that the character of the soil (light sandy loam) at Maine Prairie Road may be the principal factor favoring dominance by *N. pulchra*, or interact with the sea breeze to do so. In any case, one’s ability to generalize to vast areas of the Sacramento (and San Joaquin) Valleys where there is no corroborative evidence, either historical or contemporary, from these tiny putative relicts is called seriously into question.

From the standpoint of butterfly biology, the validity of the bunchgrass prairie concept is a serious issue. Echoing the Clementsian view, Shapiro (1984) raised the following question: “The most striking, and rather surprising, absence in the Valley grassland fauna is that of a set of specialist Satyrinae or Hesperiidae associated with the native bunchgrasses. The near-extermination of these grasses leaves little hope of finding relicts of a (totally hypothetical) pre-American fauna.” Most of the temperate grasslands of both the Northern and Southern Hemispheres have distinctive faunas of grass-feeding butterflies belonging to the two families cited above (usually one or the other is clearly dominant). Shapiro (1984) observes of Patagonia: “The large rivers coming down from the Andes and crossing the vast treeless plateaus of Patagonia are fringed with a narrow band of riparian forest, but there is essentially no butterfly fauna there... The great majority of species are Satyrids that live not in the moist river bottoms but on the steppe proper, feeding on the bunchgrasses.” There is no hint that either Satyrids or Hesperiids evolved to exploit the supposed bunchgrass prairie of the California Central Valley. This could reflect it being too recent as a community, a question best addressed by examining what little palynological record exists (although many Gramineae are not distinguishable at the generic level). But it could also reflect its not having been widespread or abundant at all.

The bunchgrass-feeding skippers *Hesperia lindseyi* Holl. and *H. columbia* Scud. occur in both the Coast Range and Sierra Nevada foothills but not on the Valley floor, nor has either been found in the Sutter Buttes. Different subspecies of a third *Hesperia*, *H. colorado* Scud. (formerly put in *H. comma* L.), occur on opposite sides of the Valley. In the absence of any relicts, the hypothesis of former cross-Valley contacts, as against dispersal along the respective mountains without crossing the Valley, might be testable using molecular phylogeography.

If bunchgrass prairie was not the dominant vegetation in this region, what might have been? The

most penetrating and thoughtful treatment of this question, based on both contemporary and historical evidence, is by Holstein (2001). His analysis has been bolstered by the publication of the book *California’s Fading Wildflowers* by Richard Minnich (2008) which, however, does not cite Holstein or Dremann though it cites the other sources cited above and many others. Minnich’s focus is primarily farther south than the Sacramento Valley, however. Summing the contemporary vegetation literature, we are led to a somewhat different picture of what the butterfly fauna of the pre-European Sacramento (and especially San Joaquin) Valley might have been.

#### A NEW INTERPRETATION OF THE VEGETATION

Enormous masses of colorful wildflowers are bound to attract attention. They are the aspect of Californian native vegetation most often noted by both early Spanish and later American explorers and colonists, but they are not the only ones. These people were intensely interested in the potential uses of the landscapes through which they passed, and routinely made note of their value as grazing land (“*pasto*” or “*zacate*”). If there were extensive tracts of bunchgrass prairie, one would expect these to be noted. Unlike the hard, coarse Patagonian bunchgrasses (“*coirones*”), Californian bunchgrasses were soft and palatable to European livestock—a fact often adduced to account for their elimination and replacement by the coarse and early-desiccating Mediterranean annuals.

In fact, as demonstrated exhaustively by Minnich (2008), bunchgrass prairie is undocumented in the Central Valley. Depending on the season, the early chroniclers report either immense blooms of [annual] wildflowers – which Minnich refers to as “forbfields” – or, after late April or May, no living vegetation at all, or “summer desert” or “summer barrens.” The pattern near the coast was quite different, with green vegetation and good pasture persisting essentially year-round. The *diseño* (map) of Rancho Tolenas in Solano County describes the slopes above the Sacramento River floodplain as *lomas muertas* (dead, i.e. barren, hills). The *diseño* for Rancho de los Molinos likewise describes the uplands as *tierra estéril* (sterile land), and so on. The introduction and naturalization of exotic annuals made relatively little difference to this pattern in the absence of irrigation. In 1844 Charles Wilkes described the Sacramento Valley as “barren and unproductive...affording but little good pasture.” John Muir wrote of the Central Valley in 1904 that “The shrunken mass of leaves and stalks of the dead vegetation crinkle and turn to dust beneath the foot, as if it had been literally cast into the oven.” Clarence

King (1915) described the Valley as “a plain slightly browned with the traces of dried herbaceous plants.” These sorts of descriptions apply to precisely the areas treated by Clementsians as bunchgrass prairie and so mapped in my 1974 Fig.2. Actual bunchgrass grasslands are documented in the foothills (where they still occur) (Fremont, 1848; Beetle, 1947). The annual forb flora that made up these ephemeral blooms broadly overlaps the surviving flora of vernal pools in the Central Valley. The vernal pool biotope, even when nearly intact and extensive as at Jepson Prairie, Solano County, at Vina, Butte County, or various locations in eastern Sacramento County, has no butterfly fauna at all, a fact documented by Shapiro and his graduate student Carrie Shaw in field surveys and remarked upon in Shapiro (1984): “The surviving vernal-pool communities in the Sacramento Valley have their specialist bees, but no butterflies.” I speculated elsewhere (Shapiro, 1975) that this was due to the year-to-year variability in the timing of a very short window of resource availability. (There are a few moths, especially Heliothentine Noctuidae feeding on either tarweeds (Asteraceae) or Scrophulariaceae *sensu lato*, successfully adapted to this very rigorous regime). There is no reason to believe the forbfields of the pre-irrigation Valley had a butterfly fauna, either. We are thus presented with the paradox of a landscape covered with brightly colored flowers, and no or very few butterflies among their visitors. Tarweeds (Asteraceae: *Holocarpha virgata* and species of *Hemizonia*), which are summer-blooming annuals, are today codominant with Mediterranean grasses over large areas that have never been plowed due to poor soils or hardpan. They are remarkably absent from the antique descriptions of the summer uplands, yet they must have been there. Unpublished observations by Shapiro in the 1970s in what is now the Stone Lakes National Wildlife Refuge near Elk Grove, Sacramento County, and in other areas with summer-dry tarweed-annual communities near Sacramento, consistently demonstrated a dry-season fauna of three butterfly species: *Junonia coenia* Hubner, *O. sylvanoides* (remarkably consistently associated with the summer-blooming forb *Trichostema lanceolatum*, Lamiaceae, to which it uniquely among our butterflies is adapted as a pollinator), and, when present regionally (as it often is not), *Pontia protodice* Bdv. & Le C. Of these, as discussed below, only *O. sylvanoides* was certainly an historic presence. One additional surviving member of the dry-summer upland flora is the Turkey Mullein, *Eremocarpus* (or *Croton*) *setigerus* (Euphorbiaceae), used as a nectar source by various butterflies and as a (strongly seasonal) larval host by the weedy multivoltine *Strymon melinus pudica* H. Edwards, which

might have had alternate, early-season hosts in the late winter-early spring forbfields.

Alternatively, one can envision highly-mobile butterfly species moving into the seasonal forbfields to exploit the abundant hostplant resources there, and then moving on. The one species that unambiguously employed, and still employs, this strategy is *Vanessa cardui* L. Shapiro (1973, 1974b, 1980) posited a regular rhythm of up- and downslope colonization by multivoltine species in pursuit of host plants in good condition. The biggest problem with such a scenario for the forbfields is getting colonists in place in late winter-early spring (since there had been no previous fall generation there). *V. cardui* is a mass migrant, but the vast majority of weedy butterflies disperse as singletons.

Holstein (2001) makes what for me is a compelling case that the dominant graminiforms of uplands in the pre-European Valley were not bunchgrasses but rhizomatous clonal species which dominated the understory of oak savanna and ecotones between the summer-dry uplands and wetlands and riparian forest. Of these the grass *Leymus* (formerly *Elymus*) *triticoides* and the sedges *Carex barbarae* and *C. praegracilis* were probably most important. Relict stands of these plants are still fairly common and able to hold their own against naturalized exotics even in my own study sites (North Sacramento, West Sacramento, Rancho Cordova and Willow Slough). *Leymus* and *Phalaris* are both used as hosts today by at least two native Valley butterflies, *Coenonympha tullia californica* Westwood & Hewitson and *Ochlodes sylvanoides* Bdv., both of which are in decline in synchrony with habitat conversion and urbanization in the Valley.

## OUT OF THE TULE?

In Shapiro (2002, 2003) and Graves and Shapiro (2003) as well as in *Field Guide to Butterflies of the San Francisco Bay and Sacramento Valley Regions* (2007), I consistently argue that the weedy, multivoltine butterfly fauna of the modern Sacramento Valley must be derived from that of the tule marshes that previously occupied extensive parts of the Valley, mainly to the east. The basic argument is that these butterflies (a) are multivoltine elsewhere and are thus unlikely to have evolved multivoltinism in the 200 years since the Valley was colonized by Europeans and (b) today feed on plants naturalized from abroad but closely related to autochthonous plants of the tule marshes, many of which are still used occasionally today in remnant wetland habitats. A few additional remarks on the marshes and the historic flooding regimes of the Valley seem useful in evaluating this scenario.

Flooding was a recurrent phenomenon in the 19th-Century Sacramento Valley. In autumn of 1837 – 12 years before the Gold Rush–Sir Edward Belcher explored the Sacramento River drainage before the onset of the rains. He wrote: “All the trees and roots on the banks afford unequivocal proofs of the power of the flood-streams, the mud-line on a tree we measured exhibiting a rise of ten feet above the present level, and that of recent date... During the rainy season, which commences about the middle of November and terminates about the end of February, the river is said to overflow its banks, when its impetuosity is such that navigation is then impossible. The annual rains do not, however, of necessity inundate these low lands, but in severe seasons, after heavy falls of snow [in the Sierra Nevada], they produce one immense sea, leaving only a few scattered eminences...as so many islets or spots of refuge.”

Charles Wilkes (1849) commented that “a large part of [the Sacramento Valley] is undoubtedly barren and unproductive, and must forever remain so. The part that is deemed good soil is inundated annually, not for any great length of time, yet sufficiently long to make it unfit for advantageous settlement.” And George Derby, who famously surveyed and mapped the region in 1849, said of the Valley between Cache and Putah Creeks (i.e. in the vicinity of modern Woodland and Davis, Yolo County): “The whole country between the creeks is liable to overflow, and is very dangerous to attempt travelling after a heavy rain. The ‘tule’ swamp, upon the western bank of the Sacramento, extending to the vicinity of Butte Creek, and occurring occasionally above, is from three to six miles in width, and impassable for six months out of the year.” It is important to note that there are abundant historical records of Sacramento Valley flooding well before the practice of hydraulic mining led to downstream siltation of the riverbeds and thus exacerbated the problem (Kelley, 1959, Thompson, 1960).

The location of the tule marshes was dictated by the unusual topography of the Valley, well described by Thompson (1960). During their overflows the rivers laid down “natural levees” raised several (5-20) feet above the surrounding plain. Tributary creeks were dammed by them and unable to reach the river directly. Their waters thus ponded up behind the natural levees, creating extensive wetlands which in the wettest years would not dry out at all. These were the tulares, named from the Spanish word for “reeds.” In very wet years the tributary streams might breach the natural levees, or the flows coming down the Sacramento River might overwhelm them. The entire system was clearly very dynamic from year to year. As early as 1848, radical reclamation projects

were proposed for the flood basins. In 1850 T. Butler King advanced specific proposals to that end. The history of implementation is complex and involves political rivalries, feuds, and violence (Kelley, 1989). Ultimately most of the marshes were drained and a system of levees and fixed weirs created which enabled the former flood basins to be used as diversion channels during periods of heavy flow, thereby sparing urban and agricultural land from flooding; during the dry season their rich alluvial soils could be farmed. This is the system in place today, and from its dynamics we can draw inferences about the biology of butterflies in the tule marshes of yore.

Half of my West Sacramento study site (see <http://butterfly.ucdavis.edu> for maps and description) lies in the Yolo Bypass, one of the diversion channel successors to the tules. During the period of my studies there, the Bypass portion has been unflooded in very dry years and flooded continuously for as long as six months in very wet ones. The non-agricultural plant communities in the floodplain include substantial amounts of native riparian vegetation, as well as many naturalized exotics. The composition of the annual vegetation is extremely labile and related to the timing of flooding and drying. Although flooding has occurred to a depth of 19 feet (5.7+ m), there are potential refuges for overwintering individuals of at least some species, in taller trees and on elevated roadway and railway supports. Flooding to a depth of 2 m or more which persists more than a few weeks appears to cause widespread mortality but only very local extinctions, while the most extreme flooding events (as in the winter of 2005-06) appear to eradicate the entire butterfly fauna over a larger area. The site is then rapidly reinvaded from adjacent upland habitats and typically experiences very rapid population growth and a multivoltine-butterfly “bloom” by late in the same season, perhaps favored by the temporary local eradication of parasitoids with poorer colonizing ability than the butterflies themselves. In the Suisun Marsh, Solano County, flooding, while frequent, is less extreme and very few (even local) extinctions have been observed in 37 years. The persistence of specialized wetland butterfly faunas elsewhere (in the humid Northeast, for example, or in the British and Low Countries fenlands) demonstrates that such faunas are well-adapted to ordinary seasonal inundation cycles. The most extreme events must have adversely impacted the pre-American butterfly fauna of the tule marshes, without however being catastrophic to them. It should be noted parenthetically that we know next to nothing about how most wetland butterflies survive inundation.

## THE IMPORTANCE OF RIVER BARS

Sand and gravel bars on the accreting sides of rivers and streams probably have had an important role as butterfly habitats in the Valley, providing a combination of strong sunshine and ready availability of near-surface water. In the contemporary Valley such bars routinely provide habitat for foothill plants otherwise not seen in the Valley today, including *Eriogonum umbellatum*, *E. wrightii*, *Penstemon heterophyllus*, *Keckiella breviflora*, *Mimulus aurantiacus*, *Mentzelia laevicaulis*, *Heterotheca oregona compacta*, *Baccharis viminea*, *Brickellia californica*, and even good-sized shrubs such as *Philadelphus lewisii*. These are mostly plants demanding a rocky or gravelly substrate, otherwise unavailable in the Valley where bedrock lies buried under thousands of feet of alluvium. Such species as *Callophrys dumetorum*, *Plebejus acmon*, *Strymon melinus* and *Erynnis persius* breed in such habitats today and may have been almost completely dependent on them in the past. This is true despite their inherent instability and vulnerability to inundation; river bar species must be good colonizers. River bars also may have provided corridors for foothill species to come down to the Valley floor: *Papilio eurymedon*, *Anthocharis sara*, *Euphydryas chalcedona*, *Chlosyne palla*, and *Ochlodes agricola* still do so without, however, being breeding residents below the lowest foothills. *E. chalcedona* breeds down to Folsom and Fair Oaks, Sacramento County, and strays from the west have been taken along the Putah Creek channel at Davis, Yolo County, but the Sierra and Coast Range foothill populations differ in a variety of ways including larval coloration, suggesting that despite their close proximity they were not in contact across the Valley floor: perhaps the tule marshes were an impenetrable barrier to them. Host plants of *Satyrium saepium* Bdv. (*Ceanothus*) and *S. tetra* Edw. (*Cercocarpus betuloides*) and of *Philotes sonorensis* Feld. & Feld. (*Dudleya*), *Mitoura johnsoni* Skin. and *M. spinetorum* Hew. (*Arceuthobium*) all occur on the lowest foothills but there is no evidence they, or the butterflies, ever existed on the Valley floor. Molecular phylogeography, as earlier noted, offers promise of testing hypotheses of prior connectivity across the Valley by what are today foothill species.

## WHAT WAS WHERE, AND DOING WHAT?

Based on the reinterpretation of the Sacramento Valley vegetation, here are scenarios for the pre-European ecologies of the resident butterfly species. Like much of “environmental history” or “Historical ecology” (Egan & Howell, 2001), these are at best

informed guesses—but perhaps better than taking the existing fauna as an ahistorical “given.” When necessary, the taxonomy has been modified from Shapiro (1974).

*Danaus plexippus* L. May have bred seasonally in the tules or along streams on *Asclepias fascicularis*. Other species of Milkweeds were certainly present in the foothills and coastwise. *A. speciosa* occurs today in riparian areas and may have in pre-American time.

*Coenonympha tullia californica* Westw. & Hew. In rapid decline today, but probably previously widespread in rhizomatous-grass riparian ecotones in the past.

*Ceryonis pegala boopis* Behr. Not recorded in the Valley today, but very likely to have occurred along streams and ecotones historically.

*Speyeria callippe* Bdv. Probably widespread where Johnny Jump-Up, *Viola pedunculata*, occurred, in vernal pool and forbfield areas. Possibly now extinct in the Valley.

*Speyeria coronis* Behr. Given its demonstrated capacity to reach the Valley, may also have been present in pre-American time, presumably also on Johnny Jump-Up.

*Phyciodes campestris* Behr. Probably common in the Delta and in the tules, with *Aster chilensis*.

*Phyciodes mylitta* Edw. Probably mostly (or entirely) a wetland species on native thistles (*Cirsium*). Until the introduction of weedy thistles this species would have had no upland summer hosts available.

*Polygonia satyrus* Edw. Essentially unchanged: tule marsh and riparian forest with its host the native nettle *Urtica holosericea*.

*Nymphalis antiopa* L. Riparian, river bars, and marshlands, on Willow (*Salix*).

*Nymphalis milberti* Latr. Riparian and marshlands, on *Urtica holosericea*.

*Vanessa atalanta* L. Riparian and marshlands, on *Urtica holosericea*.

*Vanessa virginiensis* Dru. Riparian and marshlands, river bars, on native everlastings, mainly *Gnaphalium*.

*Vanessa annabella* Field. Riparian and marshland, on *Urtica* and the native mallow *Sidalcea*. Possibly in alkali

lands on *Malvella leprosa*.

*Vanessa cardui* L. Everywhere, breeding unimpeded on native hosts (Asteraceae, Malvaceae, Boraginaceae) in spring forbfields and then moving on. This seasonal rhythm is completely consistent with its migratory pattern, and helps to explain why summer breeding is so rare and spotty in the Valley today.

*Junonia coenia* Hbn. It is not certain that this species was present in the Valley, but if so it was probably as a migrant or sporadic breeder. If *Lippia (Phyla) nodiflora* (Verbenaceae) is native—the matter remains in dispute—it could have provided a year-round resource in riparian habitats. Otherwise, all its potential native hosts (Scrophulariaceae in the broad sense) are highly seasonal. Other than *Lippia*, all its dry-season hosts today are naturalized exotics.

*Limenitis lorquini* Bdv. Riparian and marshlands, probably river bars, on *Salix*.

*Adelpha bredowii californica* Butl. Oak woodland along the margins of the Valley, and in riparian forest.

*Atlides halesus* Hbn. Riparian and oak woodland, on *Phoradendron*.

*Strymon melinus pudica* H. Edw. This weedy species might have been able to utilize a seasonal succession of hosts to be multivoltine in forbland and perhaps on river bars, though necessarily highly mobile. Candidate hosts include *Lotus purshianus*, *Eremocarpus setigerus*, and in alkali lands, *Malvella leprosa*.

*Satyrrium californica* Edw. Restricted to oak woodland and riparian forest.

*Satyrrium sylvinum* Bdv. Riparian, river bars and marshland, with *Salix*.

*Satyrrium auretteorum* Bdv. Oak woodland and oak-rich riparian forest.

*Incisalia iroides* Bdv. Possibly in riparian and tule marsh on Dodder (*Cuscuta*) and/or on uplands on Soap Plant (*Chlorogalum pomeridianum*). Both are used regionally today.

*Callophrys dumetorum* Bdv. Possibly in uplands and river bars or even forblands on either *Lotus scoparius* or *Eriogonum nudum*.

*Lycaena xanthoides* Bdv. Much of the distribution of

this species today depends on the presence of the introduced weed *Rumex crispus*, which is tolerant of drier conditions than the native *Rumex*. Its historic distribution was probably restricted to the tule marshes where native hosts would have occurred.

*Lycaena helloides* Bdv. The same restriction applies to this species; its native hosts (*Rumex*, *Polygonum*) are wetland species, while its weedy exotic hosts today allow it to occupy drier habitats.

*Brephidium exile* Bdv. Presumably restricted to alkaline and saline moist habitats where native hosts (*Suaeda*, *Salicornia*, *Sesuvium*) occur. It would be so restricted today in the absence of the roadside weed *Salsola*.

*Everes comyntas* Godt. Although it has been suggested that this species is an introduction, there is no solid evidence to support that claim. If it was present in pre-European times it could have existed in riparian habitat, using either native perennial *Lathyrus* or annual *Lotus* (e.g., *purshianus*) as hosts in various generations. *Lathyrus jepsonii* var. *jepsonii* is a marsh plant.

*Plebejus acmon* Westw. & Hew. As with *Callophrys dumetorum*, possibly in uplands, river bars and forblands with *Eriogonum nudum* and/or *Lotus* species. Also possibly with *Lotus scoparius* and/or *Eriogonum wrightii* on river bars.

*Plebejus icarioides* Bdv. I collected one specimen in West Sacramento in 1973. At that time the perennial lupine *Lupinus formosus* was still fairly common on the Valley floor, mostly along railroad rights-of-way. It is now nearly extinct regionally. This is a host plant of *P. icarioides* in the hills in Solano County and I consider it likely that it supported this butterfly until fairly recently in grassland and forbland on the Valley floor.

Holstein (2001) says: "In valley and foothill prairie remnants with soils similar to those most suitable for bunchgrasses another forb, *Lupinus formosus*... is frequent... It occurs at Stone Lakes refuge away from *Leymus triticoides* on somewhat sandier sites, is frequent on Delhi sands in Merced County, and also occurs on steep Coast Range foothills north of Fairfield in Solano County." I did not find *P. icarioides* at Stone Lakes in the 1970s, nor in the early 2000s.

*Glaucopsyche lygdamus* Dbl. Possibly occurred in tule marsh or riparian forest with native perennial *Lathyrus*, or with *Lupinus formosus* on sandy soils, or perhaps with annual lupines such as *L. succulentus* in forbfields. In

southern California this species sometimes breeds on *Lotus scoparius*. It does not use this plant here today, but if it did previously it could have occurred with it on river bars.

*Celastrina ladon echo* Edw. Status on Valley floor very uncertain, but if it did occur it would have had to have been in riparian forest, perhaps on shrubby dogwood (*Cornus*) and/or California Buckeye (*Aesculus californica*). It is not clear how deeply Buckeye penetrated the Valley floor in riparian corridors. Another host, *Ceanothus cuneatus*, occurs in riparian forest to the lowest foothills, but not on the Valley floor today.

*Apodemia mormo* Feld. & Feld. It is not inconceivable that the Mormon Metalmark occurred on sandy soils and/or river bars with *Eriogonum nudum* and/or *E. wrightii*—perhaps even in forbfields where these plants provided a second wave of bloom in late summer or autumn.

*Battus philenor* L. Riparian forest with *Aristolochia californica*, as today.

*Papilio zelicaon* Luc. Almost certainly a tule marsh species, where hosts capable of supporting more than one generation occurred – *Cicuta*, *Oenanth*.

*Papilio rutulus* Luc. Riparian forest, where preferred hosts *Platanus*, *Fraxinus* and *Salix* occur, along with preferred nectar source *Cephalanthus*.

*Papilio multicaudatus* Kirby. Riparian forest, probably with *P. rutulus*.

*Pontia protodice* Bdv. & Le C. Although a dryland-adapted species, the occurrence of the Checkered White in the Central Valley today is dependent on naturalized hosts (*Hirschfeldia incana*, *Lepidium latifolium*). There are no summer hosts in the native flora, so it is likely this species was not a breeding resident in pre-European time.

*Euchloe ausonides* Bdv. The only native Crucifer with suitable characteristics (growth form, stature) to be a pre-European host is *Guillenia lasiophylla*, now a rare plant mostly confined to railway rights-of-way, but probably a fairly common component of forbfields and, given its soil preferences, of any bunchgrass prairie that did exist. As strictly a spring species, this Pierid was well-adapted to the Valley climate.

*Colias eurytheme* Bdv. Status uncertain. The Orange

Sulphur could have been resident in the Valley by changing its host plant with almost every generation, and being highly mobile. It also could have undergone a regular seasonal altitudinal migration, of which hints persist today.

*Zerene eurydice* Bdv. Riparian forest, with its host *Amorpha californica*, now nearly extinct on the Valley floor.

*Epargyreus clarus* Cramer. Riparian forest with *Amorpha californica* and possibly *Lathyrus* and/or *Lotus crassifolius*.

*Pyrgus scriptura* Bdv. Despite the recency of the oldest museum records, I am treating this as native, in alkali lands with its sole host *Malvella leprosa*.

*Pyrgus communis* Grote. The ubiquity of this species today is an artifact of naturalized weedy hosts. In pre-European times it would have been restricted to *Malvella leprosa* in alkali lands and *Sidalcea* in the tule marshes; it could not have been multivoltine on ephemeral forbland mallows.

*Pholisora catullus* Fabr. Status uncertain; it is not clear which, if any, *Amaranthus* species occurred in the pre-European Valley, and in what habitats.

*Erynnis persius* Scud. In sandy areas and on river bars, with *Lotus purshianus*, and in riparian habitat with perennial *Lathyrus*.

*Erynnis propertius* Scud. & Burg. Riparian forest with oaks.

*Erynnis tristis* Bdv. Riparian forest with oaks.

*Atalopedes campestris* Bdv. Status uncertain; may not be native in Central Valley. Now too human-associated to infer original habitat associations.

*Ochlodes sylvanoides* Bdv. Riparian forest, tule marsh, and ecotones; bunchgrass areas; relationship to summer forbs today indicates a long association.

*Ochlodes yuma* Edw. Despite claims that this is an introduction in cismontane California, this species is treated here as native in the Delta and Suisun Marsh and perhaps more widely in the pre-European Valley, with *Phragmites*.

*Polites sabuleti* Bdv. Alkali and saline areas and possibly sandy soils and river bars, with the native perennial



turfgrass *Distichlis spicata*.

*Poaes melane* Edw. Riparian forest; native hosts unidentified.

The following species are omitted from this treatment as presumptive introductions since European colonization: *Agraulis vanillae* L., *Pieris rapae* L., *Hylephila phyleus* Dru., *Lerodea eufala* Edw.

This is a postulated fauna of 53 species. Of these four (*C. p. boopis*, *S. coronis*, *P. icarioides*, *A. mormo*) are hypothetical; three (*E. comyntas*, *P. scriptura*, *O. yuma*) have been claimed by some authors to be non-native but are assumed here to be native; and five (*J. coenia*, *P. protodice*, *C. eurytheme*, *P. catullus*, *A. campestris*) do not have well-defined pre-American host relationships, and may not have been resident. This leaves 41 species believed to be unambiguously autochthonous in the Valley. When these are broken down by inferred pre-European habitats (a species may have several), they cluster as follows: Riparian 29 (of which 6 require Oak), Tule marsh 19, River bars 10, Forbfields 7 (some with reservations), Alkali lands 6, Bunchgrass prairie/sandy soils 3. The role of summer water availability in shaping this fauna is obvious. Equally obvious is that the existence of bunchgrass prairie was never necessary to explain the characteristics of the Sacramento Valley fauna. It was, in fact, irrelevant.

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## Population biology of *Euptoieta hegesia* (Nymphalidae: Heliconiinae: Argynnini) in an urban area in Southeastern Brazil

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**Abstract.** A population of the heliconiine butterfly *Euptoieta hegesia* was studied during 15 months on the campus of the Campinas State University, SE Brazil. The data revealed a small and unstable population. The number of individuals captured per day varied from one to 10. The sex ratio was female biased. Age structure was relatively stable throughout the study, with a shift in dry season related to the low number of individuals. Average residence time was of three days for males and one day for females, with a maximum of 14 days for males and three days for females. The average forewing length of females (31.7 mm) was significantly higher than the average forewing length of males (30.5 mm). *Turnera ulmifolia* was the most common nectar source during the study. The results suggest that the individuals sampled in the study area are only part of a larger and more widely distributed population.

**Key words:** *Euptoieta hegesia*, mark-recapture, Nymphalidae, *Turnera ulmifolia*, urban ecology.

### INTRODUCTION

Although the recent surge of interest in conservation of tropical environments has led to an increase in studies of natural history and ecology of tropical organisms, there remain few population studies of butterflies to date. Most studies have dealt with species of Heliconiinae, Ithomiinae (Nymphalidae) and Troidini (Papilionidae) in forested areas (Freitas, 1993, 1996; Pinto & Motta, 1997; Ramos & Freitas, 1999; Freitas & Ramos, 2001; Freitas *et al.*, 2001; Andrade & Freitas, 2005). Few studies have been made in open habitats (but see Schappert & Shore, 1998; Vanini *et al.*, 1999).

The Heliconiinae (Nymphalidae) are a well-known and of considerable evolutionary interest, with mostly studies concentrated in the tribe Heliconiini (Turner, 1971; Ehrlich & Gilbert, 1973; Cook *et al.*, 1976; Araujo, 1980; Mallet & Jackson, 1980; Brown, 1981; Ehrlich, 1984; Romanowsky *et al.*, 1985; Mallet, 1986; Quintero, 1988) by comparison with the other tribes (e.g., Schappert & Shore, 1998; Francini *et al.*, 2005)

*Euptoieta hegesia* (Cramer, 1779) belongs to the

tribe Argynnini, subfamily Heliconiinae (following Freitas & Brown, 2004). *E. hegesia* ranges from Mexico to Argentina and the Caribbean islands, occurring in open habitats from sea level to 1200 m (DeVries, 1987). Its main larval host is *Turnera ulmifolia* L. (Turneraceae), an herbaceous weed with ephemeral flowers common to roadsides and open landscapes (Barret, 1978; Barret & Shore, 1987). Alternative host plants have been recorded (DeVries, 1987; Schappert & Shore, 1998). The only published study on population biology is the work of Schappert and Shore (1998) in Jamaica. Although their study included information on the biology of *E. hegesia* in nature and captivity, it dealt with an insular population of a restricted geographic range.

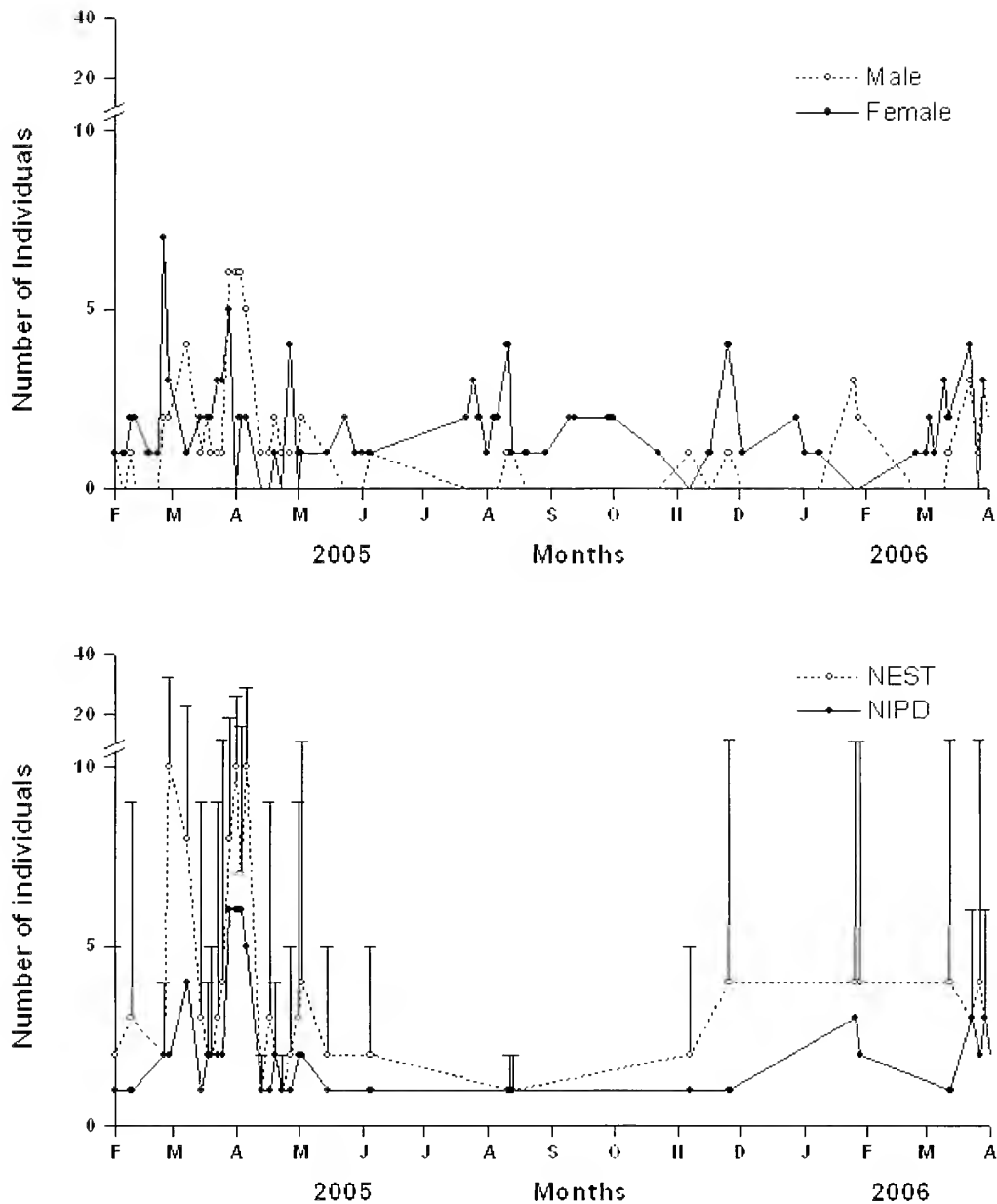
Our study describes population parameters of *E. hegesia* in an open urban habitat in southeastern Brazil, and compares them with other Neotropical butterfly species.

### STUDY SITE AND METHODS

The study was carried out on the campus of the Universidade Estadual de Campinas (Unicamp), state of São Paulo, southeastern Brazil. The study is part of a project on urban ecology at University Campus (see also Vanini *et al.*, 1999; Cogni *et al.*, 2000 and Dutra & Freitas, in prep.). Annual rainfall is 1360 mm and average temperature is 20.6°C ("Instituto Agrônomo de Campinas"). The regional climate is seasonal, with a warm wet season from September to April and a cold dry season from May to August. During the period of study the average temperature of the coldest month

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**Figure 1.** Above, number of males and females of *E. hegesia* collected from February 2005 to April 2006. Arrows indicate mechanized grasscuttings. Below, population size (males only) of *E. hegesia* as number of individuals present per day (NIPD) and Lincoln-Petersen estimates, from February 2005 to April 2006. Arrows indicate mechanized grass cuttings (for both pictures). Vertical bars = standard error.

was 18°C and of the warmest month was 24°C.

The study site is a typical University campus habitat, composed of wide lawns with sparse trees and scattered small flowering shrubs, separated by buildings and streets. Lawns were mowed by campus crew five times during the study period (10 II 2005, 17 IV 2005, 26 VIII 2005, 28 IX 2005 and 8 II 2006).

Population parameters were estimated by mark-release-recapture (MRR). Butterflies were netted,

numbered on the underside of one forewing with a felt-tipped pen, and released at the point of capture. Sex, wing length and place of capture were recorded for each. Marking provided estimates of population size and individual movements (Cook *et al.*, 1976; Turner, 1971; Freitas, 1993, 1996; Ramos & Freitas, 1999). Forewing length was measured to the nearest millimeter with a ruler. Age was estimated visually and recorded using a three category system (new,

intermediate and old) modified from Ehrlich and Davidson (1960), Brussard and Ehrlich (1970) and Ehrlich and Gilbert (1973).

Butterflies were captured from 8 II 2005 to 12 IV 2006, 1-3 times per week, for a total of 67 field days. Marking sessions were conducted with 1-2 persons for about two hours and always between 0830 h and 1330 h.

MRR data were analyzed by the Lincoln-Petersen method, with Bailey's modification for estimating population parameters of population size and standard errors, using CMLR software developed by Dr. R. B. Francini, Unisantos.

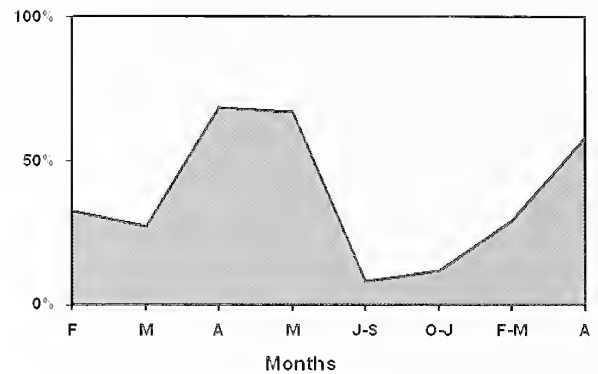
Daily results are presented as "number of individuals present per day" (NIPD), with recaptured individuals considered as present in the population over all previous days since the day of first capture (= risk marked animals, as in Ramos & Freitas, 1999 and Vanini *et al.*, 1999). Residence time was estimated following Brussard *et al.* (1974). Sexes were analyzed separately in most cases.

## RESULTS

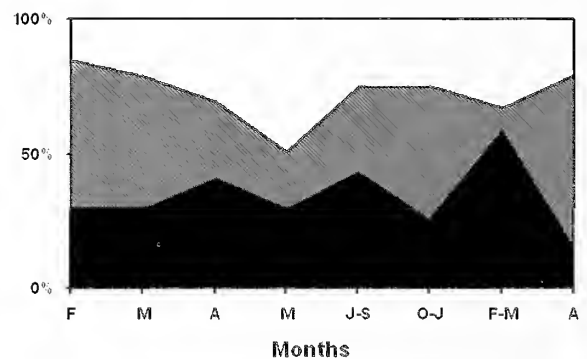
**Population biology.** A total of 159 individuals of *Euptoieta hegesia* (50 males and 109 females) were captured between February 2005 and April 2006, with 23 of these recaptured one or more times. The number of individuals captured per day varied from 0 to 7 (mean = 1.94; SD = 1.71; n = 67) for males and from 0 to 7 (mean = 1.72; SD = 1.31; n = 67) for females (Fig. 1). The estimated number of males present per day varied from 1 to 10 (mean = 3.79; DS = 2.63; n = 33) (Fig. 1). The population (based on individuals present per day) peaked during March and April 2005.

**Sex Ratio.** Sex ratio was highly female biased ( $X^2 = 21.89$ ; DF = 1;  $P < 0.0001$ ), with the proportion of males to females changing over the months (Fig. 2). All recaptured females (n = 6) were recaptured only once, while males were recaptured up to three times (n = 17). The proportion of males recaptured (39.5%) was significantly higher than of females (5.5%) ( $\chi^2 = 22.49$ ; DF = 1;  $P < 0.0001$ ).

**Age structure and residence time.** The age structure of the population remained stable during the study (Fig. 3). However, there was an increase in the proportion of older individuals in May versus intermediate ones, reaching approximately 50% of the total individuals. In February and March of 2006 there was a peak of new individuals, corresponding to 58% of the sample. The average estimated residence time for males was three days (maximum of 14 days) and for females was one day (maximum of three days).



**Figure 2.** Sex ratio of *E. hegesia* represented by the percentage of males from February 2005 to April 2006.



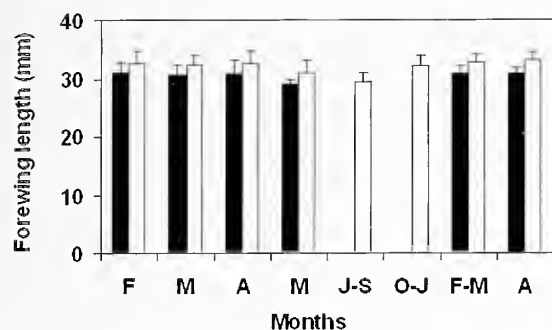
**Figure 3.** Age structure of individuals of *E. hegesia* from February 2005 to April 2006. Black = new; gray = intermediate; white = old individuals.

**Wing size.** The average forewing length of females (32.4 mm, SD = 2.22, n = 106) was significantly longer than of males (31.7 mm, SD = 1.85, n = 49) ( $t = 3.51$ ; DF = 155;  $P < 0.001$ ) (Fig 4). The variation of wing size through the year suggests a reduction in the size of the individuals after April of 2005, rising again between October of 2005 and January of 2006.

**Resource.** *E. hegesia* was observed visiting four different nectar sources during the study: *T. ulmifolia* (Turneraceae), *Tridax procumbens* L., *Emilia sonchifolia* (L.) DC. (Asteraceae) and *Lantana camara* L. (Verbenaceae). Of 68 records, 59% were on *T. ulmifolia* and 34% on *T. procumbens* L.

## DISCUSSION

Contrasting with populations of *Heliconius* that maintain relatively constant numbers throughout the



**Figure 4.** Average forewing length of males and females of *E. hegesia* from February 2005 to April 2006. Vertical bars = standard deviation. Black bars = males; white bars = females.

year (Turner, 1971; Ehrlich & Gilbert, 1973; Araujo, 1980; Ramos & Freitas, 1999), the results for *E. hegesia* suggest an unstable open population at the study site. Even with the proportion of recaptured males relatively high, females were seldom recaptured and appeared to have flights of long range, suggesting that the individuals in the study area were only a fraction of a larger and more widely distributed population. Lawn mowing during the study period appeared correlated with a reduction in number, as was observed in April. Lawn mowing eliminates immatures and most of the adult food sources. The effect may in turn have caused dispersion of adults to neighboring habitats, producing the abrupt reduction of butterfly number observed. Since lawn mowing occurs across the entire Campus and in urban lots, adults can re-colonize the study area coming from these neighboring sites when resources are also there eliminated. Mowing may accordingly explain the abruptly variation in butterfly numbers and the inconstant population pattern found. A similar pattern was observed in *Evrema elathea* (Cramer, 1777) (Vanini *et al.*, 1999).

The preponderance of female captures contrasts with the usual male-biased captures in field studies with butterflies, including *E. hegesia* itself (Brussard & Ehrlich, 1970; Freitas, 1993, 1996; Schappert & Shore, 1998; Ramos & Freitas, 1999; Freitas & Ramos, 2001; Freitas *et al.*, 2001; Vanini *et al.*, 1999; Andrade & Freitas, 2005). Male biased sex ratios are usually explained by differences in behavior between the sexes, with males flying in the same places as collectors, the trails with nectar resources (Freitas, 1996; Ramos & Freitas, 1999). When this collecting bias is removed, sexes may be sampled in proportion to their actual occurrence in natural habitats, for example using bait traps (Uehara-Prado *et al.*, 2005; Uehara-Prado

& Freitas, 2008) or by sampling the entire area where adults occur, as in the present study where there is no place to hide.

Age structure remained constant throughout the period of study, indicating the lack of a specific recruitment time. However, the apparent "aging" of the population observed during May 2005 may indicate a lower recruitment of new individuals, with the local population sustained by butterflies born the prior month. The maximum observed lifespan supported the study of Schappert and Shore (1998).

Schappert and Shore (1998) also noted that females were significantly larger than males. Although the observed variation in wing size for both sexes was low, the smaller average values observed from May to September may correlate with changes in the nutritional quality of larval foodplants. When the rainy season begins during October and the plants become robust, wing length also increase.

The frequent use of the flowers of *T. ulmifolia* contrasts with the study of Schappert and Shore (1998), who found this nectar source not commonly used by *E. hegesia*. In our study, *E. hegesia* appears to use all available flowers across the study site as food, which is likely a consequence of few alternative nectar sources and high prevalence of *T. ulmifolia* across the study site. The same pattern of nectar use of was found to *E. elathea* in the same area (Oliveira, 1996).

In the literature, no general pattern is revealed with butterfly species in open habitats. Thus population structures can be different in different populations of the same species as well as in the same population in different years (Ehrlich, 1984). In some species of nymphalids, for example, population structure may vary among local populations occurring in discrete demographic units (Dowdeswell *et al.*, 1957; Brussard *et al.*, 1974) to open populations spread over wide areas (Brussard & Ehrlich, 1970). In our study area, the instability of larval and adult resources caused by of the periodic mowing of the lawns may force the high vagility of adults and may at the same time also select more mobile individuals. The result explains the large, open, and widespread population in the study area and neighboring landscapes.

A broader study program, with additional labor and multiple sites around the study area, would be necessary to clarify the regional pattern of population dynamics in the region. Moreover, the interaction of these results with other ecology studies done on the campus would be useful to establish a more rational policy of handling green areas of the campus, aiming for maximizing biodiversity. The latter is an obvious indication of the health of urban ecosystems with maximal biodiversity the goal (Brown & Freitas, 2003).

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## Observations of overwintering nymphalid butterflies in underground shelters in SW and W Bohemia (Czech Republic) (Lepidoptera: Nymphalidae: Nymphalini)

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**Abstract.** The results from ten years of surveys and observations of overwintering nymphalid butterflies in various types of underground shelters in SW-W Bohemia, Czech Republic are presented. During these surveys, three species of nymphalid butterflies were encountered; the most commonly observed species was *Inachis io* (Linnaeus), followed by *Aglais urticae* (Linnaeus). *Nymphalis polychloros* (Linnaeus) was encountered in the ten year period only twice. The typical overwintering sites for *Inachis io* were the ceilings of unheated cellars of buildings, and the entrances of mining tunnels/galleries or natural caves. A special category of underground shelters in the study area was abandoned World War 2 military bunkers. *Inachis io* frequently hibernates in aggregations of several individuals and *Aglais urticae* does so less often. The lowest ambient air temperature measured in these underground shelters was  $-1.1^{\circ}\text{C}$ . It is believed that these observations represent the longest continuous record of hibernating nymphalid butterflies in underground (or other) shelters in Czech Republic.

**Key words:** phenology, ecology, overwintering sites, winter diapause, hibernation, Anglewing butterflies, butterfly conservation, natural resource protection

### INTRODUCTION

The Anglewing butterflies are a small group of nymphaline butterflies inhabiting the Northern Hemisphere (ca. 35 sp.). It is generally agreed that this group is a natural monophyletic clade, based on several synapomorphic characters including special adaptations that enable the adults to survive the winter in hibernation (hibernal diapause) (see Scott, 1979). Recent phylogenetic studies (Nylín *et al.*, 2001; Wahlberg & Nylín, 2003; Wahlberg *et al.*, 2005) confirmed the monophyletic relationship for the Anglewing butterflies as a group. For the purposes of this paper we recognize the genera *Aglais*, *Inachis*, *Nymphalis*, and *Polygonia*. However, it may turn out that there are only two genera: *Aglais* and *Nymphalis* comprise the Anglewing butterflies. If that is the

case, then *Inachis* would become a junior subjective synonym of *Aglais* and likewise *Polygonia* becomes a junior subjective synonym of *Nymphalis*. For the purposes of this paper we recognize the genera *Aglais*, *Inachis*, *Kaniska*, *Nymphalis*, *Polygonia* and *Roddia*. The genus *Kaniska* is not represented in Europe, and the Euro-Asian *Roddia l-album* does not occur recently in Bohemia. There are a few more or less anecdotal notes regarding overwintering nymphalines from Bulgaria (Beshkov & Petrov, 1996), former Czechoslovakia (*cf.* Košel, 1984; Dvořák, 2000, 2002), France (Sarlet, 1982), Germany (Bronner, 1987; Herhaus & Karthaus, 1996), Poland (Kowalski, 1955), Spain (Escola, 1982) and others. This paper reports observations of primarily *Inachis io* (L.) and *Aglais urticae* (L.).

With the onset of fall, typically at the end of August, these butterflies begin to search for suitable overwintering shelters. Depending on the species, the selected sites vary. The most frequently observed

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overwintering shelters include crevices beneath roofing shingles; animal burrows; cavities in hollow trees; rock and branch piles; attics, barns and other outbuildings; unheated cellars; caves; and mining tunnels and galleries. Once in the shelter, the butterfly falls into a stupor as the temperature drops. The freezing point of their cell tissue is lowered by an increased content of glycerols and sugars, which act as an antifreeze (Pullin & Bale, 1989a, b). The freeze tolerance seems to vary between species, as evidenced by the selection of different wintering sites. Using electrical conductivity, K. W. Philip (pers. com.) found that adults of *Nymphalis antiopa* in Fairbanks, Alaska do not freeze until the temperature reaches  $-30^{\circ}\text{C}$ . In the spring, the hibernal diapause is broken when a period of cold weather passes.

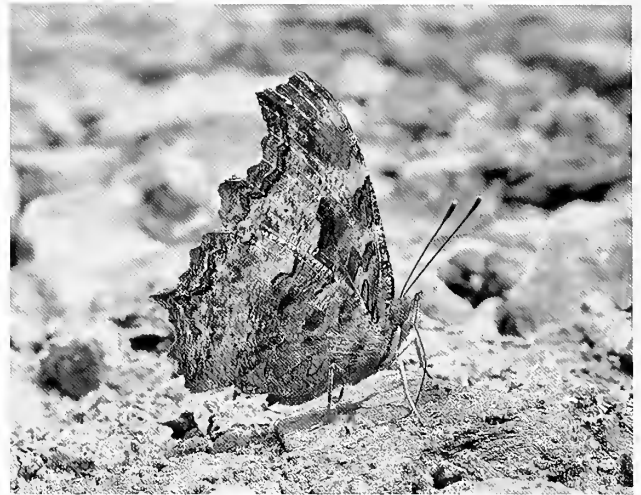
Most butterflies typically live no longer than thirty days, but some overwintering butterflies can live up to almost a year (Guppy & Shepard, 2001). This remarkable longevity is a direct adaptive product of adult hibernal diapause.

An immobile butterfly is very vulnerable to discovery by a predator (Wiklund & Tullberg, 2004). To minimize the detection by birds, mice and other predators, Anglewing butterflies have evolved cryptic coloration and pattern on the ventral side of their wings (Fig. 1). In normal posture, the hibernating butterfly folds its wings over its back, exposing only the ventral side. This minimizes its silhouette and butterfly blends in with the background (camouflage).

## SURVEY METHODS

### Study area and wintering sites

The overwintering sites visited during the surveys included underground shelters such as caves, mining tunnel and gallery entrances, military bunkers, and unheated cellars of castles, monasteries, and residential houses. A few natural karstic, pseudokarstic and/or fissure caves were also visited. The 10-year observation period started in the winter of 1994–1995 and continued until the winter of 2003–2004. Altogether, 347 locations were surveyed in this period. Some of locations were visited only once; some of them were visited several times during one winter. A total of 2265 visits were made in this period. Table 1 summarizes the wintering sites and localities. The total number of wintering butterflies was recorded during each visit to each site. In one instance, a long mining tunnel was surveyed in five metre intervals for all wintering Lepidoptera. Some results have been previously partly reported by Dvořák (2000, 2002).



**Figure 1.** *Nymphalis j-album*, Cummington Fairgrounds, Hampshire County, Massachusetts.

### Hibernating Butterfly taxa

Most Czech butterflies overwinter as pupae or larvae. Of the 161 species recently reported for Czech Republic by Beneš *et al.* (2002), only the nine species are known to overwinter as adults. These are: *Gonepteryx rhamni* (L.) [Pieridae: Pierinae], *Nymphalis polychloros* (L.), *N. xanthomelas* Esper, *N. l-album* Esper, *N. antiopa* (L.), *Inachis io* (L.), *Aglais urticae* (L.), *Polygonia c-album* (L.) [all Nymphalidae: Nymphalinae: Nymphalini]. Of these, *N. l-album* and *N. xanthomelas* do not occur in SW Bohemia. *Polygonia c-album*, which hibernate in central Europe, evidently do not hibernate in underground shelters (Wiklund & Tullberg, 2004). One specimen was found on the wall to the entrance to the cellars of the Přečín castle in SW Bohemia on 31.XII.2006 (L. Dvořák, unpubl. data).

Other allied nymphalid butterflies, such as *Araschnia levana* (L.) hibernate as pupae; and the vanessids, such as migratory *Vanessa cardui* (L.), apparently do not hibernate at all (Pollard *et al.*, 1998); *V. atalanta* (L.), which is also migratory, can occasionally hibernate in central Europe (Tucker, 1991; Hensle, 2000). It is interesting to note that Schappert (2000) observed *Vanessa atalanta* and *V. virginiensis* in mid-March in Ontario, Canada, in addition to overwintered individuals of *Nymphalis antiopa*, *N. j-album*, *Aglais milberti*.

Over a period of 10 years, individuals of three species – *Aglais urticae*, *Inachis io*, and *Nymphalis polychloros* – were observed using various underground shelters as their hibernation sites. Table 1 summarizes the observations.



## Statistics

We analysed the occurrence of nymphalids in wintering shelters by general linearized models (GLM) with a Poisson distribution of the dependent variable (number of individuals) separately for each species, using S-Plus 2000 package (Splus, 2000, 1999). To delimit effects of space autocorrelation, we included variables of place and space to all models. The effect of differences due to year was entered into analyses both as a continuous and as a categorical variable.

## RESULTS

### Nymphalids in different shelters

Three species, *A. urticae*, *Inachis io*, and *N. polychloros*, were found in the underground shelters in the study area. However all three species were found together only in the abandoned military bunkers. These bunkers are typically concrete structures, partially buried in the ground. The species most frequently encountered there was *Inachis io*, which seems to hibernate there very regularly (more than 82% from 45 visited bunkers). *Aglais urticae* was the next most frequent species (almost 18% of locations). This is the only shelter type where three hibernating individuals of *Nymphalis polychloros* were found. In the natural caves, only a few hibernating individuals of *Inachis io* were found. This species was found in four out of 18 caves. *Inachis io* used more than one-third of 139 tunnels/galleries; *Aglais urticae* occurred there only marginally, with two records only. In unheated cellars, *Inachis io* was the typical species (more than one-half of 145 locations), while *Aglais urticae* was rarer there (15% of locations only) (see Table 1).

*Inachis io* was the most numerous species in all types of overwintering shelters. It prefers bunkers but also regularly occurs in cellars. On the other hand, this species uses tunnels/galleries very sporadically; natural caves were the only other hibernation place recorded. Although the microclimatic conditions appeared to be very similar there, those shelters apparently are not as suitable for this species.

*Aglais urticae* has overwintering preferences similar to those of *Inachis io*. The primary difference in the results is that *A. urticae* is rarer in the study area than *I. io* and it also uses other, above ground, shelters for hibernation. *Aglais urticae* was recorded 11 times by itself, without the presence of *Inachis io* during the same visits, and 64 times together with *I. io*.

*Nymphalis polychloros* was found only on two separate occasions in military bunkers. At present, this species is the rarest species in the study area (Dvořák, pers.

**Table 1.** Summary of underground overwintering sites for Anglewing butterflies in the Czech Republic (W and SW Bohemia) - 10 years of records (winters of 1994/5-2003/4).

	# of sites	# of visits	Average	Maximum
<b>Bunkers:</b>				
	45	197		
<i>Inachis io</i>	37 (82%)	105 (53%)	6.2	28
<i>Aglais urticae</i>	8 (18%)	21 (11%)	2.7	11
<i>Nymphalis polychloros</i>	2 (4%)	2 (1%)	1.5	2
<b>Caves:</b>				
	18	109		
<i>Inachis io</i>	4 (22%)	5 (4.6%)	3.2	9
<b>Tunnels/Galleries:</b>				
	139	1336		
<i>Inachis io</i>	49 (35%)	232 (17%)	2.3	43
<i>Aglais urticae</i>	2 (1%)	2 (>1%)	1	1
<b>Cellars:</b>				
	145	623		
<i>Inachis io</i>	83 (57%)	271 (43.5%)	5.6	66
<i>Aglais urticae</i>	22 (15%)	52 (8.4%)	2.4	9
<b>Total:</b>				
	347	2265		
<i>Inachis io</i>	173 (50%)	613 (27%)	4.4	66
<i>Aglais urticae</i>	32 (9%)	75 (3%)	2.5	11
<i>Nymphalis polychloros</i>	2 (0.6%)	2 (0.1%)	1.5	2

#### Explanation of Table 1.

**Bunkers** – abandoned military concrete bunkers, mostly from World War 2 but some more recent.

**Caves** – natural karstic, pseudokarstic and fissure caves.

**Tunnels/Galleries** – entrances of abandoned mining tunnels and galleries.

**Cellars** – unheated cellars of houses, castles and monasteries.

**Total** – reported for all categories of overwintering shelters.

**Numbers (#) of sites** – total number of shelters surveyed with number of shelters (percentage in brackets) occupied by individual species (e.g. 45 bunkers were checked and 37 of them had *Inachis io*).

**Numbers (#) of visits** – total number of visits to any one type of shelter and number of positive checks (percentage in brackets) for each species (e.g. out of 197 checks of bunkers, 105 were positive for *Inachis io*).

**Average** – the average number of butterflies per site that had hibernating individuals present.

**Maximum** – the maximum number of specimens of each species observed in a single overwintering site.

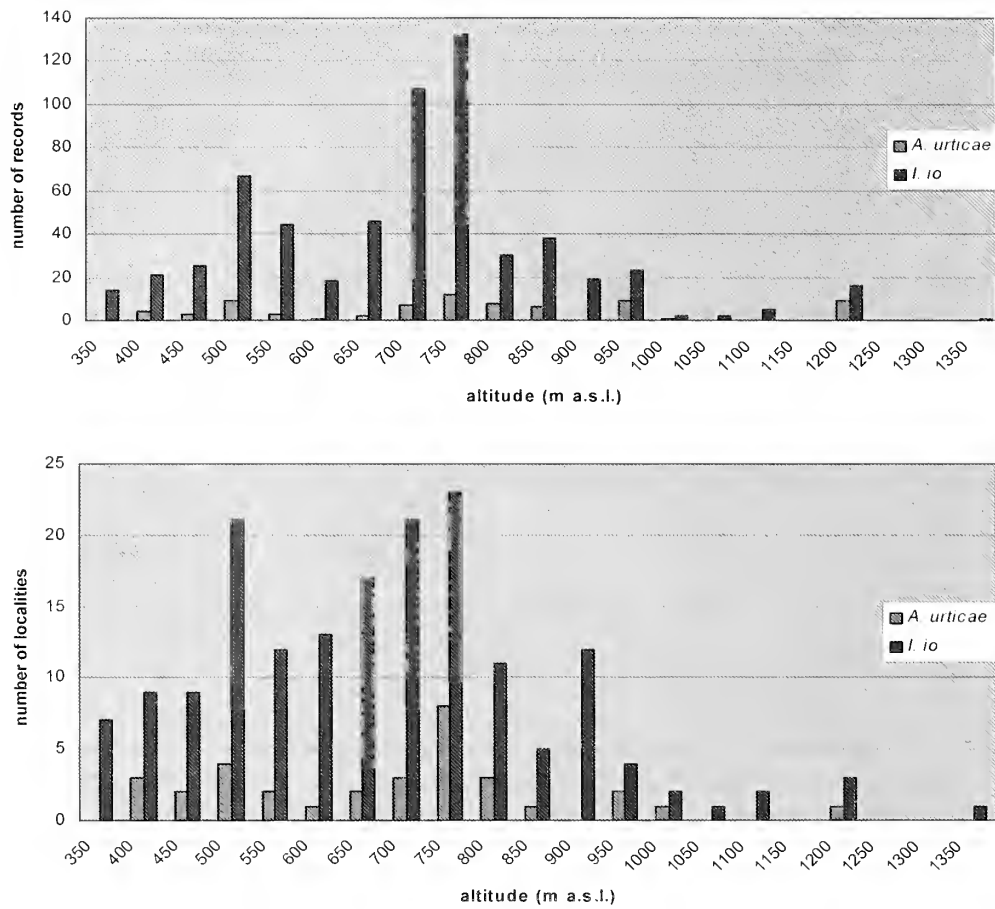


Figure 2. Comparison of abundance of *Inachis io* and *Aglais urticae* at different elevations.

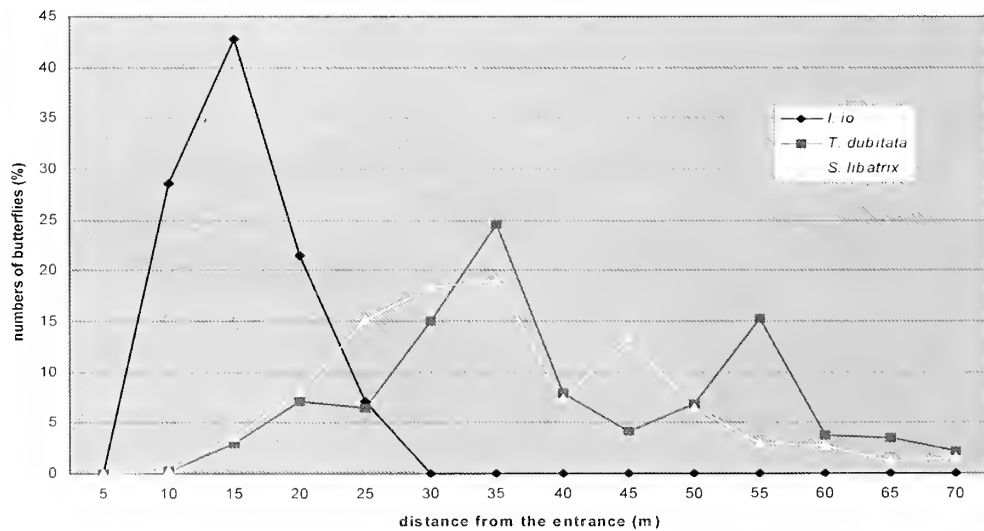


Figure 3. Comparison of abundance of *Inachis io* and two moths (*Scoliopteryx libatrix*, *Triphosa dubitata*) by distance from the entrance of one limestone gallery.

**Table 2.** Mass overwintering roosts (W and SW Bohemia) - maximum numbers found.

Locality:/Species:	Date	# individuals
<i>Inachis io</i>		
Klášter Teplá, cellars of a monastery	31.I.2003	66 ex.
Zhůří, cellars of a house, nr. Huťská Hora Mt.	18.X.1996	48 ex.
Okrouhlá, cellars of a fort	24.II.2003	47 ex.
Amálino Údolí, mining tunnel/gallery "Sněmovní"	23.XI.1995	43 ex.
Zhůří, cellars of a house, nr. Huťská Hora Mt.	13.XI.1997	41 ex.
Kašperk, cellars of a castle	5.XII.1996	38 ex.
<i>Aglais urticae</i>		
Záhvozdí, military bunker SE of the village	13.IX.1998	11 ex.
Záhvozdí, military bunker SE of the village	15.XI.1998	9 ex.
Klášter Teplá, cellars of a monastery	2.II.2004	9 ex.
Zhůří, cellars of a house, nr. Huťská Hora Mt.	7.IV.2004	9 ex.
Ostroh, cellars of a castle Seeberg	3.II.2004	7 ex.

observation). The closely related species *N. antiopa* is more common than *N. polychloros* in Bohemia. The fact that *N. antiopa* was never found in the underground shelters - although the rare *N. polychloros* was - indicates that the two species do differ in hibernation sites, and that *N. antiopa* may not use underground shelters at all.

### Hypsometric distribution

Both *Aglais urticae* and *Inachis io* have a visible peak in number of overwintering records at an altitude 500 and 750 m a. s. l., judging from number of records and number of locations (Fig. 2). This result may be strongly influenced by the fact that the majority of shelters were in those altitudes, however it apparent the occurrence curve is the similar for both species. Fig. 2 corroborates the conclusion that both species have similar requirements for underground winter shelter, and probably the only difference is that *I. io* is the more common species of the two.

### Numbers of individuals

A large number of individuals were found hibernating together in only some underground shelters. In several locations, congregations were found repeatedly for several consecutive years. For some locations the dates of visits are listed, together with the greatest numbers of wintering butterflies (Table 2). From those data it is also evident that (i) both species prefer cellars and/or bunkers and (ii) *A.*

*urticae* is less frequently found in underground shelters than is *Inachis io*.

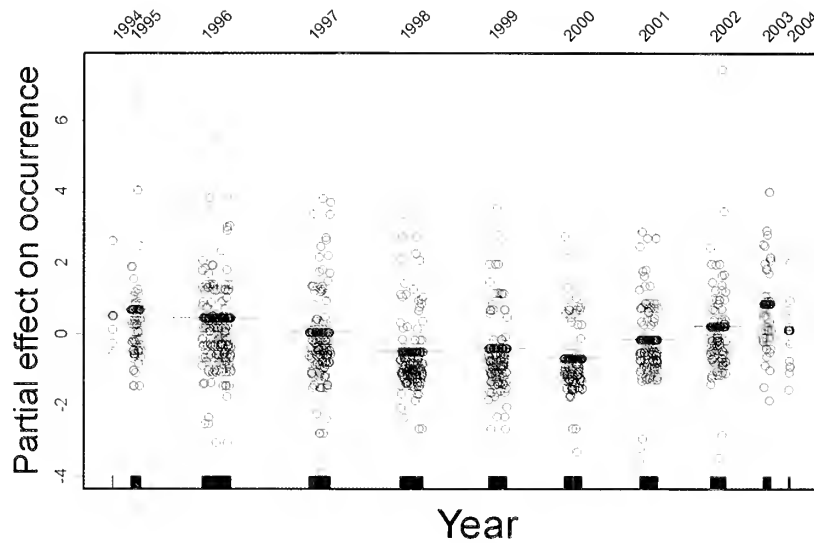
### Temperature

The air temperature in the shelter is one of the factors significantly influencing the overwintering of Nymphalini (Pullin & Bale, 1989a, b). *Inachis io* was found during winter in shelters at temperatures between  $-1.1$  and  $+14.6^{\circ}\text{C}$ . It is interesting to note that *I. io* was found hibernating relatively close to the entrance of the gallery, in contrast to the winter diapausing moths *Scoliopteryx libatrix* and *Triphosa dubitata*, whose occurrence peaked about 15 m in from the entrance (Fig. 3).

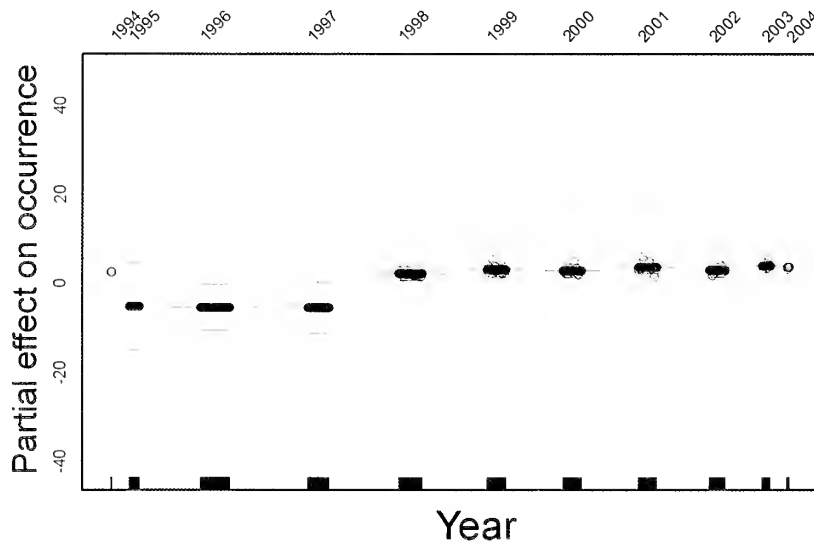
### Differences between years

We found very strong differences between the occurrence of *Inachis io* and *Aglais urticae* in different years ( $F_{10, 1330}=14.95$ ,  $p<<0.0001$  and  $F_{10, 1330}=85.4$ ,  $p<<0.0001$ , respectively). For the analyses, the most reasonable was entering year as the factor variable. For *I. io*, when year was treated as a continuous variable, it explained 0.7% of the variability; when year was treated as a categorical variable, it explained 12.9% of the variability. For *A. urticae*, when year was treated as a continuous variable, it explained 30.8% of the variability; when year was treated as a categorical variable, it explained 49.5% of the variability. This means that between-year variation is strongly irregular, with the pattern much more complicated in *I. io* than in

## Inachis io



## Aglais urticae



**Figure 4.** Effect of between-year variation on occurrence (in natural logarithms) of *Inachis io* and *Aglais urticae* in underground shelters, after filtering out the effects of place and site.

*A. urticae* (Fig. 4). There was also a strong correlation between occurrence of *I. io* and occurrence of *A. urticae* ( $F_1, 1339=11.18, p < 0.001$ ).

## DISCUSSION

It appears that *Vanessa atalanta* is not an obligatory

hibernator in the Czech Republic (Belicek, pers. observations), and hence this species was not observed hibernating during this study. According to Higgins and Riley (1978) and others, these butterflies either migrate south or die during autumn in Europe. One of the few published records of overwintering individuals of *V. atalanta* was from a military bunker NW of Krefeld

(Hülser Bergrs foothills, western Germany). One individual was found hibernating there on 19.I.1997, together with individuals of *Aglais urticae* and *Inachis io*, by Bäumler in Hensle (2000). Another case of hibernating *V. atalanta* is from a graphite gallery/mining tunnel in the study area, but this is observation is more than 30 years old (Majer in Dvořák 2000).

From the observations made over a 10-year period, it seems likely that *Nymphalis polychloros* only very rarely hibernates in underground shelters. Dvořák found one individual of this species in a natural cave of the Bohemian Karst (central Bohemia) that was in summer aestival diapause (Dvořák, 2002). The two records reported here from abandoned military bunkers in the Bohemian Forest foothills (SW Bohemia) are the first documented examples from the study area.

It is often stated that *Aglais urticae* partly immigrates into the region from the south, and that the immigration is supplemented by local hibernation. Underground shelters probably represent only a part of the spectrum of shelters used. The species is rarely found in natural caves of central Europe (cf. Kowalski, 1955; Bronner, 1987). *A. urticae* was not found in any cave visited in the study area. There are very few published observations from other underground shelters. Several specimens were observed hibernating in Germany, e.g. in hollows of highway bridges in Oberberg region (Herhaus & Karthaus, 1996) or in bunkers (Hensle, 2000). As far as known to us, no mass winter roosts of this species have been reported in the literature. The observed congregations of up to 11 individuals reported here are noteworthy.

On the other hand, records of hibernating *Inachis io* from different underground shelters are relatively numerous; being reported also from caves (e.g. Kowalski, 1955; Košel, 1984; Dvořák, 2002) and other underground shelters. The highest number reported was 46 individuals in one bunker (Hensle, 2000), and up to 60 individuals in a cavity of a highway bridge (Herhaus & Karthaus, 1996). The 66 individuals found in a cellar of a monastery was the highest number recorded in this survey.

## CONCLUSIONS

The three nymphalid species *Inachis io*, *Aglais urticae*, and *Nymphalis polychloros* were observed using underground shelters in SW and W Bohemia as their overwintering sites.

*Inachis io* was the most common species in underground shelters, while *Aglais urticae* was less numerous.

Unheated cellars and abandoned military bunkers were the predominant wintering sites, followed by entrances to mining tunnels/galleries. A few records of *I. io* were from natural caves.

*Inachis io* was commonly observed in mass aggregations in winter shelters (up to 66 individuals), while groups of *Aglais urticae* were found only occasionally and in smaller numbers.

Only three specimens of *Nymphalis polychloros* were found individually in abandoned military bunkers.

In terms of butterfly conservation and protection of natural resources, it is apparent that wintering sites such as abandoned military bunkers, entrances to mining tunnels/galleries, caves, etc. are important for the winter survival of these butterflies. Consequently, well known wintering sites should be protected during the winter from undue disturbance.

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## APPENDIX



1. *Aglais urticae*, in cellars of a monastery in Teplá, W Bohemia, February 2004, photo J. Bartoš.
2. *Inachis io*, in an abandoned military bunker near Opolenec, SW Bohemia, January 2004, photo M. Rudlová.
3. *Nymphalis polychloros*, in an abandoned military bunker near Tuškov, SW Bohemia, January 2004, photo V. Vlk.
4. A building of a former hotel in Bečov nad Teplou, W Bohemia, February 2003, hibernation place of *Inachis io* and *Nymphalis polychloros*, photo V. Vlk.
5. The Entrance to an underground gallery near Kašperské Hory, SW Bohemia, May 2004, in cellars were found hibernating *Inachis io* and *Aglais urticae*, photo J. Bartoš.
6. An abandoned military bunker near Tuškov, SW Bohemia, May 2004, hibernation place of *Inachis io*, photo V. Vlk.

## A revised classification scheme for larval hesperiid shelters, with comments on shelter diversity in the Pyrginae.

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**Abstract.** The construction of larval leaf-shelters is a ubiquitous yet poorly understood behavior within the HesperIIDae. Most life history papers treating this family fail to describe this aspect of larval behavior in detail, despite its potential usefulness for comparative ecological and phylogenetic studies. Here, using 15 years of experience rearing Neotropical skippers, I present a means of describing the five basic types of shelters built by hesperiids. In addition, I provide a preliminary look at the distribution of these types within the subfamily Pyrginae and discuss ideas for informative areas of future research.

**Key words:** behavior, HesperIIDae, larval shelter, leaf-shelter, shelter architecture, shelter construction

### INTRODUCTION

The construction of leaf shelters by exophytic lepidopteran larvae is a widespread phenomenon within the order (DeVries, 1987, 1997; Frost, 1959; Scoble, 1992; Stehr, 1987). A few studies have examined the process of shelter construction (Fitzgerald *et al.*, 1991; Fitzgerald & Clark, 1994; Fraenkel & Fallil, 1981; Rensch, 1965), while others have investigated the ecological forces which shape the evolution of this remarkable life history trait and its associated behaviors (but see Eubanks *et al.*, 1997; Henson, 1958; Jones, 1999; Jones *et al.*, 2002; Loeffler, 1996; Ruehlmann *et al.*, 1988; Sagers, 1992; Sandberg & Berenbaum, 1989; Weiss, 2003). The construction of most lepidopteran larval shelters is accomplished primarily by harnessing the forces generated by axial retraction of stretched and wetted silk (Fitzgerald *et al.*, 1991) and frequently, particularly in the HesperIIDae, the substrate is further modified during the process by cutting (e.g., Fitzgerald & Clark, 1994; Greeney & Chicaiza, 2008; Greeney & Jones, 2003; Ide, 2004; Weiss *et al.*, 2003).

The globally distributed (with the exception of New Zealand and Antarctica) family HesperIIDae includes species whose larvae roll, cut, fold, and tie portions of their foodplant into a diverse array of shelter types (Greeney and Jones 2003). In fact, the remarkable radiation of shelter architectures found within this family, ranging from simple leaf rolls to complex, origami-like tents, rivals the architectural diversity

of the entire rest of the Lepidoptera. Despite this, and though natural historians have remarked upon these incredible structures for more than 100 years (e.g., Moss, 1949; Scudder, 1889; Young, 1985), only recently have they received more detailed attention (e.g., Greeney & Warren, 2003, 2004, 2008a, 2008b; Lind *et al.*, 2001; Weiss *et al.*, 2003).

Within the HesperIIDae, shelter architecture varies greatly between genera and even between larval instars (e.g., Greeney & Warren, 2004; Lind *et al.*, 2001), yet within a species the process is stereotyped (e.g., Weiss *et al.*, 2003), and various aspects of basic shelter form and ontogenetic changes in shelter style, in combination with foodplant use, vary predictably between genera, and are often useful characters for identifying larvae in the field (Greeney & Jones, 2003; Moss, 1949). While the key to hesperiid larval shelter types provided by Greeney and Jones (2003) provides us with a useful beginning, our understanding of evolutionary patterns of shelter architecture remains in its infancy. In particular, we lack a detailed understanding of which characters may prove to be phylogenetically informative. Here I supplement the observations of Greeney and Jones (2003) with further observations from throughout the Americas, as well as published descriptions in the literature.

### MATERIALS AND METHODS

In addition to reviewing published literature for hesperiid shelter descriptions, I made observations on the larval shelter building behavior of hesperiids in a variety of habitats, in various localities, in the United States, Mexico, Costa Rica, and Ecuador. In order to

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avoid potential laboratory artifacts affecting shelter construction, I include only observations made in the field or from photographs taken *in situ*. Whenever possible, I reared examples of all species observed through adult eclosion and identified them with the help of G. T. Austin and A. D. Warren. For many species, however, I was unable to attain an adult. For these, using 15 years of experience rearing hesperiid larvae, plus online photographs provided by sites such as Dyer and Gentry (2002), Dyer *et al.* (2005), and Janzen and Hallwachs (2006), I identified all larvae to subfamily, and many to genus. For discussions of shelter construction and form I have used terminology presented by Greeney and Jones (2003).

## RESULTS

Modifications to Greeney and Jones (2003). After careful consideration of the characters used to construct the dichotomous key to basic shelter types (Greeney & Jones, 2003), and extensive observations on the process of shelter construction, I have modified the existing key in the following ways (see Appendix A).

First, the three final shelter types given by Greeney and Jones (2003) (Types 8-10) are lumped as one shelter type, unified by the use of two major cuts (Greeney & Jones, 2003) in their basic construction. After watching numerous species construct two-cut shelters, it appears that the location of cut initiation (either on the same or opposite sides of the leaf mid-vein) depends, to a great extent, on the morphology of the leaf. For example, a larva on a thin grass blade, which is scarcely broader than the larva itself, has little choice but to initiate cuts on opposite sides of the leaf blade. For this reason I have chosen to lump "Type 8, two-cut folds" under a general two-cut shelter type (Appendix A). Second, the degree to which the distal portions of the two major cuts converge alters the shape of the shelter lid (the resulting folded-over flap). With some experience, the shape of the lid may be a useful character for separating species or genera in the field, but is variable and generally does not include quantifiable parameters. For this reason I have eliminated the "Type 9, unstemmed fold" and "Type 10, stemmed fold" shelter types from the classification of Greeney and Jones (2003), placing them under the broader heading of two-cut shelters (Appendix A).

The third change to the classification of Greeney and Jones (2003), recently discussed by Greeney and Sheldon (2008), is the unification of "Type 3, multi-leaf shelters" and "Type 4, two-leaf shelters." During construction of a shelter involving more than one leaf, in all species that I have observed, the larva rears back onto its prolegs, waving its thorax and head about until

it comes in contact with another usable object. Silk is then spun between this object and the leaf on which the larva is resting. In the field this object is most often another leaf or leaflet of the food plant, but is occasionally another part of the same plant (ie. stem, flower), parts of an adjacent non-food plant, or even nearby detritus. Similar observations by other authors, in the field and in the lab, suggest this is a widespread method of shelter construction (eg., Atkins, 1987; Clark, 1936; Jones, 1999; Scudder, 1889; Williams & Atkins, 1997; Young, 1993). As silk is deposited, and portions of the plant are drawn together, other foliage is often incidentally brought closer as well. As the larva flails its head about it subsequently comes in contact with this newly-reachable foliage and incorporates it into the shelter. Similarly, due to the morphology of certain food plants, one cannot move a single leaf or leaflet without displacing several. Thus, what may have been initiated as a two-leaf pocket, often incidentally or superficially involves several leaves. For most species that I have observed that build shelters involving more than one leaf, even the same individual, forced to build several shelters in a row, may switch between the previously defined "Type 3" and "Type 4" shelters. Thus, if they include two or more leaves, it is prudent to lump both "two-leaf pockets" and "multi-leaf pockets" under a single category of multi-leaf shelters.

The fourth major change to the previous classification is to include "Type 7, one-cut slide" with "Type 6, one-cut fold" shelters. I have not seen a second example of a one-cut slide shelter, even within the same species (unknown Pyrginae), and separation of the two types is unwarranted. The penultimate alteration is to eliminate "Type 1, rudimentary shelter" from the classification scheme. Few authors have mentioned species which apparently do not build shelters (e.g., Scudder, 1889; Moss, 1949), and my own observations suggest that even these may have been in error: the observed larvae were simply in-between shelters or feeding away from their shelters at the time of observation. In any case, if non-shelter building species are rigorously documented in the future, there seems little reason to call them anything other than "non-shelter builders!"

Lastly, Greeney and Jones (2003) divided all shelter types into three "groups" based on the number of cuts involved. This is a superfluous division and should be eliminated.

Diversity of shelter types in the Pyrginae. The pyrgines show by far the greatest diversity both in basic shelter form as well as types and combinations of post-construction modifications. In fact, even in my limited sampling, I have found that all major proposed shelter



types are built by species of Pyrginae. Here, though there are still many groups un-sampled, I discuss the pyrgine genera which I have observed to build each shelter type, and briefly comment on their behaviors and modifications.

**Type 1, no-cut shelters.** This is perhaps the least common shelter type built by pyrgines. In a single species of *Aguna* feeding on *Bauhinia* (Leguminaceae), which I have worked with in eastern Ecuador, later instars fold an entire leaf in half along the midvein, slowly eating their shelter away from the edges as they grow. Early instars simply move into the middle of the two halves of new leaves, while they are still folded, thus avoiding the difficulty of having to manipulate large portions of the leaf. Generally only a few lines of securing silk are needed to maintain the young leaves in their folded position. With the exception of this species, however, most pyrgine Type 1 shelters I have observed are built during later instars. Examples include *Astraptes*, *Epargyreus*, *Polygonus*, *Proteides*, *Carrheues*, and several species included in or related to the genus *Mylon*. Middle instars of *Epargyreus clarus* (Jones, 1999; Lind *et al.*, 2001) often roll the margin of the leaf into a tube without making any cuts. This type of cut often ontogenetically precedes Type 2 multi-leafed shelters in the final instars of the genera mentioned above. These tube-like shelters are sometimes modified with secondary cuts that allow the larva to seal one end of the tube.

**Type 2, multi-leaf shelters.** This shelter type is commonly seen in later instars of a variety of pyrgine genera including *Achlyodes*, *Antigonus*, *Astraptes*, *Bolla*, *Capila*, *Dyscophellus*, *Eantis*, *Epargyreus*, *Eracon*, *Eryunis*, *Gesta*, *Grais*, *Narcosinus*, *Ocyba*, *Phocides*, *Polygonus*, *Polythrix*, *Ridens*, *Tagiades*, *Theagenes*, and *Urbanus*. It is perhaps the most commonly observed shelter type within the group, but seems confined to later instars. Often, as was the case for an unknown pyrgine feeding on a bipinnate legume in Amazonian Ecuador, the leaves of the host plant are too small to build a shelter of any other type. The larva is forced to draw multiple leaves or leaflets together until there is sufficient vegetation to hide it from view. As I have observed in *Epargyreus clarus* feeding on *Robinia* (Leguminaceae) and in an unknown *Urbanus* feeding on *Desmodium* (Leguminaceae) the small leaflets of the host are quickly outgrown by later instar larvae, and more than one must be used to cover the larva.

**Type 3, center-cut shelters.** Unlike the ubiquitous use of this shelter by early instars of the Pyrrhopyginae (e.g., Burns & Janzen, 2001), there are relatively few genera of pyrgines which build this shelter type. They include *Atarnes*, *Bolla*, *Capila*, and *Noctuana*, as well as several genera which I have been unable identify. The

use of this type of shelter may reveal a great deal about the ecology and evolution of these taxa, as it appears to have arisen multiple times within the subfamily, and is built by species feeding on a wide variety of plants.

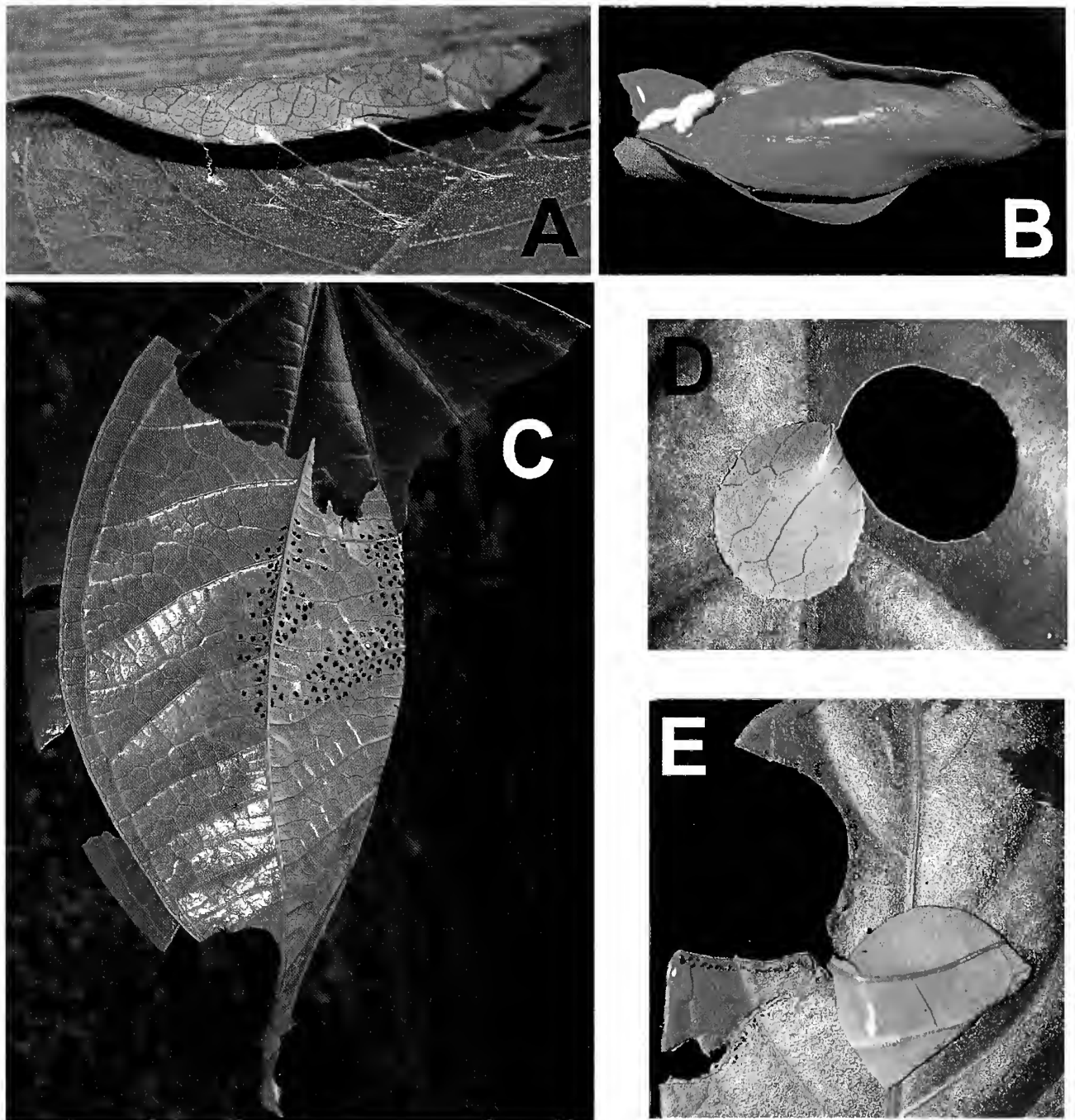
**Type 4, one-cut shelters.** One-cut shelters are seen in a small number of pyrgines including *Quadrus*, *Pythonides*, and *Systasea*. They are also built occasionally by middle instars of *Astraptes* and by several species related to (or members of) *Carrheues*, *Pyrgus*, and *Mylon*.

**Type 5, two-cut shelters.** This is one of the most common and variable shelter types seen in both early and late instar pyrgines, and often includes post-construction modifications along with a wide diversity of primary cut patterns. Type 5 shelters are built by species of *Achlyodes*, *Astraptes*, *Atarnes*, *Bibasis*, *Bolla*, *Bungatotis*, *Capila*, *Celaenorrhinnus*, *Cephise*, *Chrysoplectrum*, *Coladenia*, *Drephalys*, *Dyscophellus*, *Eantis*, *Entheus*, *Epargyreus*, *Eracon*, *Hesperopsis*, *Morvina*, *Mylon*, *Nascus*, *Phocides*, *Plumbago*, *Polythrix*, *Sostrata*, *Tagiades*, *Telemiades*, *Theagenes*, *Udranomia*, *Urbanus*, and *Xenophaeus*. The shelter lids, or excised portions of the leaf, created during construction of this shelter type vary considerably in shape. They range from nearly round to square, rectangular, or triangular. Subsequently, most are modified in some way by scoring, notching, or perforating, giving the interested natural historian a rich array of characters to choose from when comparing shelters built by various species.

## DISCUSSION

While the details of shelter architecture and the plethora of subsequent modifications to the basic form would allow for a great expansion of the shelter key provided by Greeney and Jones (2003), its utility is best enhanced by reducing it down to the most basic types. These can be applied to describing ontogenetic changes in shelter type between instars (e.g., Greeney & Warren, 2004; Lind *et al.*, 2001) as well as describing broader patterns between taxa. Modifications to these few basic types, such as perforations, channels, and notching (e.g., Greeney & Jones, 2003; Greeney & Young, 2006; Young, 1991), as well as ontogenetic changes in basic shelter types (e.g., Graham, 1988; Greeney & Warren, 2004; Lind *et al.*, 2001; Miller, 1990), can then be used as additional phylogenetic characters. As recently pointed out by Greeney and Sheldon (2008), the "devil is in the details," and even superficially similar shelters may prove to be formed by different architectural innovations which are only obvious when the detailed behaviors of shelter construction are described (e.g., Weiss *et al.*, 2003).

Behavioral and natural history characters are



**Figure 1.** Photographs of the five proposed basic shelter architectures built by hesperiid larvae. **a)** Type 1 shelter built by late instar *Astraptes* sp. **b)** Type 2 shelter built by late instar *Polygonus* sp. **c)** Type 4 shelter built by late instar *Quadrus* sp. **d)** Type 3 shelter built by early instar pyrrophygine **e)** Type 5 shelter built by early instar *Celaenorhinnus* sp.

frequently used to create and test phylogenetic hypotheses in a variety of taxa (e.g., Hennig, 1966; Lanyon, 1988; Zyskowski & Prum, 1999). Perhaps one of the most useful phylogenetic characters that can be derived from larval shelters is the ontogenetic change in shelter types. The sequence of shelter types built

during larval development can be ascertained from most thorough life history papers which take the time to describe shelter ontogeny (e.g., Greeney & Warren, 2008a, 2008b). As an example, the character state for *Noctuana haematospila* would be 3,3,5 according to Greeney and Warren (2004). This, however, provides

us only with a single, unordered character. More useful would be five characters derived from the type of shelter built by each instar. As various instars of many species often remain in the shelter built during the previous instar (e.g., Atkins, 1975, 1987, 1988; Greeney & Warren, 2008a, 2008b), these characters are unavailable for the majority of species. From my own experience with several species, procuring these data can be time consuming and frustrating. When removed from their shelter, larvae often wander a great deal before building another. In addition they may take several hours to construct a new home. In the field then, if one does not follow each larva until they at least begin construction, they may be difficult to relocate once you have released them. Anyone with the means to carry out such studies can greatly advance our understanding of shelter building for even the most common species.

In a few species for which I have made careful observations, the ontogenetic switch between shelter types may occur sometime during the middle of the instar. For example, a recently molted fourth instar *Pyrrhopyge papius* will build a Type 5 shelter. When removed from its shelter late in fourth instar, however, it will build a Type 2 shelter (unpublished data). Thus it is important to carefully note the exact stage of development before performing experiments. This type of mid-stadia switch in shelter construction, however, would be an informative line of research.

Except for the age-related variation just mentioned, all species I have observed are consistent in the basic shelter type they construct during each instar (see also Weiss *et al.*, 2003). Modifications to the basic structure, however, can be variable, even within an individual. For example an early fourth instar *Bolla tetra* building a shelter on a mature leaf may use a scoring cut to weaken the shelter bridge before folding the lid. The same individual on a younger leaf may skip the scoring cut, presumably because the softer tissue is easier to manipulate. In the case of recording shelter modifications, therefore, it may be necessary to observe several individuals to get a good measure of behavior for a species or instar. An additional important point is that often modifications occur hours or days after the basic shelter is completed. For example a fifth instar *Telemiades antiopae*, which fed while constructing its Type 5 shelter, did not begin making channels in the shelter lid until a few hours after completion of the basic structure (unpublished data). Similarly, the number and extent of shelter perforations made by *Quadrus cerialis* and *Eracon paulinus* larvae slowly increase as the shelter is occupied longer (unpublished data).

An additional area of investigation, which was first observed and described for *Epargyreus clarus*

(Weiss *et al.*, 2003), is the form and function of the silk "template" pad which all larvae I have observed spin before beginning to create a shelter. Through observations of multiple species in the field, I have noticed that the shape of this pad, which larvae use to position their bodies during cutting (Weiss *et al.*, 2003), may vary greatly between species, but is highly conserved between individuals or species building the same basic shelter type. This study should encourage others to take the time to investigate the details of shelter construction behavior and architecture in other species, even those which are common and apparently "well studied" (see Greeney & Sheldon, 2008).

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## APPENDIX A

### Dichotomous key to larval shelter types (modified from Greeney & Jones, 2003).

- 1a. Shelter construction involving one or more cuts in the leaf ..... 3  
 1b. Shelter construction not involving cutting of leaf (with the exception of post-construction feeding damage or modifications) ..... 2  
 2a. Only one leaf involved in shelter construction, typically a rolled leaf, one folded in half along the mid-vein, or simply the margin

- curled over or under slightly ..... (**Type 1; no-cut shelter**; Figure 1a)
- 2b.** More than one leaf, leaflet, leaf-lobe, or plant part involved in the shelter construction ..... (**Type 2; multi-leaf shelter**; Figure 1b)
- 3a.** At least one cut begins from the leaf margin ..... **4**
- 3b.** No cuts are initiated from the leaf margin, shelter usually rounded and folded over a narrow section forming a man-hole-cover-like lid ..... (**Type 3; center-cut shelter**; Figure 1d)
- 4a.** Shelter construction involving only one major cut, cut begins at leaf margin, resulting flap curled, folded or slid over away from its original position ..... (**Type 4; one-cut shelter**; Figure 1c)
- 4b.** Shelter with two major cuts, cuts originating from leaf margin, resulting shelter may be flattened, tubular, or hang from the apex of the leaf ..... (**Type 5; two-cut shelter**; Figure 1e)
-

## Preliminary field survey of butterflies on Xishan Hill (Kunming, Yunnan Province, China)

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**Abstract.** The survey recorded 80 butterfly species on Xishan Hill, including eight species listed on the "China Species Red List (IUCN List)." Of the species found, 51.3% are of Oriental origin, 40.0% are cosmopolitan, 6.3% are Palearctic and 2.5% are endemic to Yunnan. Pieridae and Nymphalidae are the best represented families on the hill. Among nine surveyed habitat types, edges of the primary forest and open grassland shrubs are the two most favored areas. Amongst available nectar sources Asteraceae species were most visited. Information on active periods and non-floral food was recorded. Unlike with previous studies in this area, this survey provides information concerning ecological aspects besides a checklist.

**Key words:** butterflies, species, taxonomic composition, faunal composition, habitat types, habitat affinities, active periods, feeding habits, checklist.

### INTRODUCTION

Butterflies are conspicuous insects in Yunnan Province, represented by over 600 recorded species (Lee, 1995). Prior work showed that Yunnan butterflies appear to consist of: 330 Oriental species (76.4%), 39 Palearctic species (9.0%), 63 species (14.6%) considered to be cosmopolitan, and 91 species which are (21.1%) endemic to Yunnan (Li, 1996). This community represents a distinct highland butterfly fauna.

Based on the climatic and plant community characteristics, the Yunnan butterfly fauna can be further divided into three subregions and many corresponding districts: (1) the tropical rainforest and monsoon forest subregion, including Hekou District, Jinghong District, Mengding District, and Ruili District; (2) the subtropical evergreen broadleaf forest, coniferous, and broadleaf-coniferous mixed forest subregion, including Nanpanjiang River District, Lancangjiang River District, Qujing District, and Jinshajiang River District; and (3) the temperate coniferous forest subregion, including Hengduanshan Mountain District and Zhaotong District (Li, 1996).

Kunming belongs to the second of these three. From its northern to its southern parts, Kunming is located between the Nanpan River district and Qujing district. The mean elevation is 2,000 m, with hills and low mountains. Annual mean temperature is 12~17°C; annual mean rainfall is 1,300mm (Li, 1996).

Xishan Hill lies 15 km southwest of Kunming, beyond Dianchi Lake. Xishan Hill, with an altitudinal transition from 1,900 m to 2,356 m and microclimate shift occurs with this altitudinal transition. Xishan Hill has a complicated ecology which is able to sustain a broad diversity of plants, insects, birds, and mammals. The original forests were composed of *Cyclobalanopsis glaucooides* (Wu & Raven, 2001, 2003), *Quercus variabilis*, *Q. aliena*, *Alnus nepalensis*, *Keteleeria evelyniana*, *Michelia yunnanensis*, *Pyraecantha fortuneana*, *Rhododendron* sp., *Myrica nana*, and *Piris formosa* (Wu *et al.*, 1987). Secondary forests are composed of pine trees and cypress trees. In addition, patches of farmlands exist. The mosaic of plant diversity provides for the rich butterfly community on the hill.

The recorded community of butterflies on Xishan Hill was 77 species with the following taxonomic composition: four species (5.2%) of Papilionidae, 20 species (26.0%) of Pieridae, five species (6.5%) of Danainae, 11 species (14.3%) of Satyrinae, 19 species (24.7%) of Nymphalinae, three species (3.9%) of Riodinidae, eight species of (10.4%) Lycaenidae, and seven species (9.0%) of Hesperidae (Lee *et al.*, 1995). The Acraeinae was included in family Nymphalinae at that time by Preston-Mafham and Rod (1988) who also regarded the several subfamilies of Nymphalidae as families. The present field survey here emphasizes on the ecological aspects of butterflies.

### MATERIALS AND METHODS

#### Field Sites

The field survey was carried out in the forest areas

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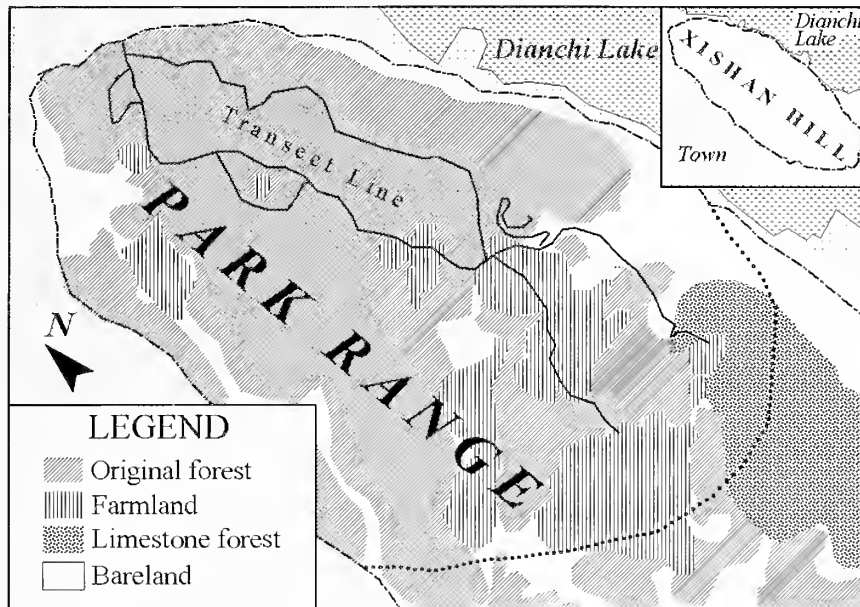


Figure 1. Map of surveyed area.

on Xishan Hill (Fig. 1), mainly along the paths in Maomao Qing and the backyard of Huating Temple. Additionally, many turnoffs and farming patches deviating from the paths were surveyed. All are shown as the transect in Fig. 1.

### Collecting methods

I walked an 18 km transect route with an altitudinal transition from 1,900 m at the foot to 2,342 m once a week from mid May to late August in 2001, from early July to late September in 2002, from late February to late April in 2003, from mid June to mid October in 2005, and from early March to mid November in 2007. The field survey had a cumulative total survey time of 470 hours.

Butterflies were caught in flight with nets, at rest on attractants, or on the ground. Traps baited with rotting bananas and mangos were used to trap some nymphalines and satyrines with every trap checked at the end of the weekly field survey. All of the collected butterflies were killed with ethyl acetate and stored in paper envelopes for later identification and as vouchers.

Plant specimens were collected with butterflies when needed. Appropriate parts (flowers, leaves, or fruits) were collected or photographed for identification.

Geographical data were recorded by a GPS device (Garmin eTrex Vista [v 3.2]).

### Specimen identification

Most butterflies were identified by sight when obvious. Undetermined specimens were later compared with determined specimens from my private collection or with field guide illustrations. Problematic specimens which did not match were studied further by microscopic observation of the adult male external genitalia.

Well known and familiar plants were identified directly in the field, but most identification was done in the laboratory using literature manuals or colleagues' help.

### RESULTS

The collected and recorded materials are presented with a series of tables and charts.

### Habitat types

I partitioned and classified nine types of habitats, from 1,900 m to 2,340 m as follows:

(1) Dense primary forest: Dominants are *Pinus yunnanensis*, *Keteleeria evelyniana*, *Alnus nepalensis*, and *Cyclobalanopsis glaucoides*. The community shows less sunlight, but higher relative humidity than the following habitat types. The understory of this habitat has grasses and bushes, especially *Eupatorium adenophorum* and *Myrica nana*.

**Table 1.** Taxonomical and faunal compositions of surveyed species.

Family	Species	Faunal catalogue			
		Palaearctic	Oriental	Cosmopolitan	Endemic
Papilionidae	10		4	6	
Pieridae	17	2	5	10	
Danainae	6		4	2	
Satyrinae	13		8	3	2
Nymphalinae	17	1	8	8	
Acraeinae	1		1		
Riodinidae	2		2		
Lycaenidae	7		5	2	
Hesperiidae	7	2	4	1	
Subtotal	80	5	41	32	2

(2) Primary forest edge: the edge area of adjoining patches of forest has a higher diversity, exemplified by shrubs and herbaceous plants such as *Gynura segetum*, *E. adenophorum*, *E. fortunei*, *Bidens pilosa*, *Taraxacum sp.*, *Pyracantha fortuneana*, *Michelia yunnanensis*, *Rhododendron sp.*, *Piris formosa*, and *Vicia cracca*.

(3) Open bare land: this type of habitat has little vegetation being mainly dust, sand and small rocks. When the dust mixes with water, the dissolved mineral salt attracts many nymphalines and skippers. Also the high morning temperature at these sites appears very attractive to butterflies during morning hours.

(4) Open farmland: crops here are mainly *Raphanus sativum* and *Brassica campestris* usually with many *Vicia cracca* vines among the crops. The crops are host plants of some pierids and their flowers also produce quantities of nectar that attracts butterflies. Many *Pieris sp.*, *Papilio sp.*, and lycaenids like *Heliophorus brahma* were noted.

(5) Open fields with grasses and shrubs: this habitat is complex with high floral diversity (where not invaded by *E. adenophorum*). The lower stratum consists of grasses and some small herbs as *Taraxacum sp.*, *Rhododendron sp.*, and *V. cracca*. The middle stratum is tall grasses and the upper stratum is a community of *G. segetum*, *P. fortuneana* shrubs and some *M. yunnanensis*. Flowers of these plants provide rich nectar sources.

(6) Dry valleys: these places are exposed to high sunlight, but low humidity, especially with southern exposures. Consequently, few xerophytes plants occur that can tolerate water deficiencies, i.e communities of *Bidens pilosa*, *Rhododendron sp.*, *Cephalanoplos segetum* and *Taraxacum sp.*. The major groups of associated butterflies are some lycaenids and nymphalines and a

few satyrines. A few swallowtails were seen but not taken.

(7) Valley with water sources: such sites are always hot and dry, so any water may attract many insect species. Wherever streams flow many swallowtails, pierids, nymphalids, riodinids, lycaenids, and skippers are present.

(8) Open sites with water: as valleys with water the sites are attractive to most butterflies.

(9) Shaded places: shaded places have their own butterfly groups that avoid sunlight. For example, riodinids and satyrines are present in shaded areas more than in other habitats.

The detailed relationship between butterfly species and habitat types are given in Fig. 3, Appendix 1.

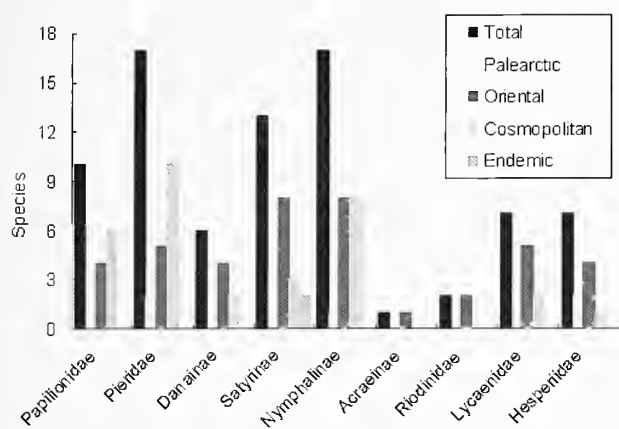
### Checklist and Red List species

During the cumulative field work on Xishan Hill, I collected 80 species of butterflies which are included in all six butterfly families (Appendix 1), all of which have been identified (Chou, 1994, 1998).

All of species were catalogued by two characteristics: faunal and taxonomic composition. The faunal composition is: 6.3% Palaearctic species, 51.3% Oriental species, 40.0% cosmopolitan species, and 2.5% species endemic to Yunnan (Chou, 1994). Taxonomic composition is: 12.5% Papilionidae, 21.3% Pieridae, 46.4% Nymphalidae (7.5% Danainae, 16.3% Satyrinae, 21.3% Nymphalinae, 1.3% Acraeinae), 2.5% Riodinidae, 8.8% Lycaenidae, and 8.8% Hesperiidae. These are cited in Table 1, Fig. 2.

Among the collected butterflies are eight species





**Figure 2.** Taxonomical and faunal compositions of each family and subfamily.

**Table 2.** Species listed on the Red List.

Species	Categories
Papilionidae	
<i>Byasa hedistus</i>	VU
Pieridae	
<i>Hebomoia glaucippe</i>	NT
Satyrinae	
<i>Ypthima nikara</i>	NT
<i>Lethe anderson</i>	NT
<i>Ypthima sakra</i>	NT
<i>Ypthima iris</i>	VU
<i>Ypthima dromon</i>	VU
Hesperidae	
<i>Lobocla proxima</i>	NT

Categories: VU: vulnerable, NT: near threat

listed on the "China Species Red List" Table 2 (Wang & Xie, 2005).

### Active period

The butterflies of Xishan Hill showed clear and distinct active periods within groups (Table 3). *Papilio xuthus*, *Colias erate*, *Pieris sp.*, *Vanessa sp.*,

*Dodona durga* and *Heliophorus brahma* are the earliest emerged species in early spring (late February). *Pieris sp.*, *Vanessa sp.*, *Laupides boeticus*, and *Celastrina oreas* are the last surviving species by early winter (early November). Most species were flying in March and were absent in October. Danaines were first seen in April and skippers appeared in May. *Actaea issoria* appeared over less than three months, from late July to early September, but the data are based on only two female specimens. For most species there is a gap between spring and summer generations. In May, only few adult butterflies were flying, and some species disappeared temporarily. These gaps may well be due to sparse data and annual variation.

### Habitat affinities

As mentioned above, nine habitat types were classified for the field survey. My conclusions on habitat affinities were based on observed butterfly species collected in each of these habitats.

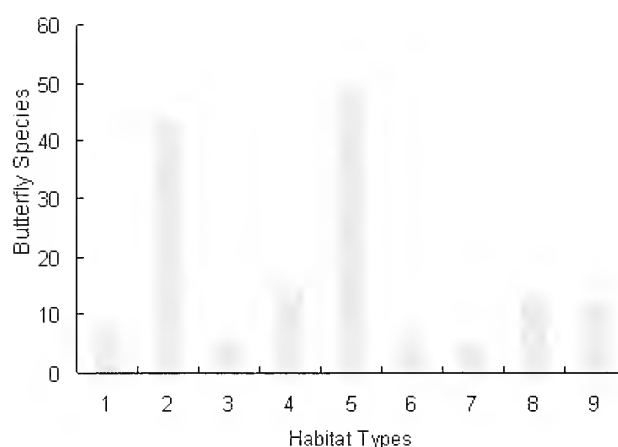
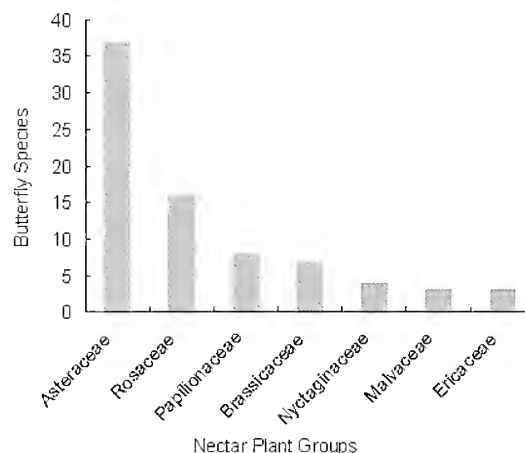
The edges of primary forest and open space with predominant grasses and shrubs are the favored habitats, the likely result of high vegetation diversity along the edges that provide the greatest number of host plants for early stages. Open land with many shrubs provides adults with rich nectar sources. Many swallowtails, pierids, danaines, lycaenids, and skippers are found in these habitats in addition to a few nymphalines and satyrines. Habitats with the lowest butterfly abundance and diversity are dry places as open bare land and dry valleys. In these places, I only found *Vanessa sp.*, *Dodona durga*, and *Heliophorus brahma* during early morning hours. Dense forest and shaded places share common characteristics in spite of vegetational differences: lower sunlight, lower temperature, and higher relative humidity. Satyrines, especially the rarely seen *Lethe spp.* and *Neope yaua*, are most common in these sites. Sites with water always provide for some butterflies during the summer, with the most common species being *Byasa polyeuctes*, *Papilio bianor*, *P. xuthus*, *Delias belladonna*, and *Aporia agathon*. Farmlands are special and most usually monoculture plantations of *Brassica caupestrus* and *Raphanus sativus* that provide fragrance and nectar during summertime.

### Feeding behavior

Butterflies which prefer flowers include all the swallowtails, all the pierids, all the danaines, plus a representation of satyrines, nymphalines, lycaenids, and skippers. Most butterflies across the study site feed on flowers. Among them, a diversity of nectar plant

**Table 3.** Major active periods of butterflies in each family and subfamily.

Butterfly families	Months										
	F	M	A	M	J	J	A	S	O	N	
Papilionidae	X	X	X		X	X	X	X	X		
Pieridae	X	X	X	X	X	X	X	X	X	X	
Danainae			X		X	X	X	X	X		
Satyrinae		X	X	X	X	X	X	X	X		
Nymphalinae	X	X	X		X	X	X	X	X	X	
Acraeinae						X	X	X			
Riodinidae	X	X	X	X	X	X	X	X	X		
Lycaenidae	X	X	X		X	X	X	X	X	X	
Hesperiidae				X	X	X	X	X	X		

**Figure 3.** Relation between species abundance and habitats.**Figure 4.** Visitation rate of major nectar plants by family.

preferences obviously exists (Table 4). Swallowtails prefer *Eupatorium spp.* and *Rhododendron spp.* Sometimes they also feed on *Vicia cracca*, *Bougainvillea glabra*, and *Hibiscus mutabilis*. Danainae prefer various Asteraceae plants which give off powerful odors, especially *Gynura segetum*. Pierids prefer farming patches, as these provide many flowering legumes, cabbages, and radishes. The remaining groups prefer flowers of small plants, including *Taraxacum sp.*, *Crepis sp.*, *Youngia sp.*, and *Potentilla fulgens* (Fig. 4).

Only a few butterflies showed a preference for non-floral attractants (Table 5). The commonest attractants were organic substances containing various acids, including rotting fruits, feces (mainly horse feces and urine), and all manner of rotting organic garbage dumped by tourists. Most nymphalines, satyrines, and lycaenids were attracted to rotting

materials. Mud also attracted many butterflies during hot summer days.

## DISCUSSION

The 80 surveyed species were collected in the areas adjacent to the routes randomly taken by insect net and in traps. There were a few areas not investigated, and their specialized species could be absent from the checklist. It should also be recognized that there were two possibly incorrectly named species among those surveyed, based upon comparison of the male genitalia with available illustrations. The two species were identified as *Heliophorus brahma* and *Ahlbergia chalcidis* (Wang & Fan, 2002).

Graphing cumulative species number against

**Table 4.** Species collected or observed on flowers.

Plant species	Butterfly species
Asteraceae	
<i>Eupatorium fortunei</i>	<i>Byasa polyeuctes</i> , <i>B. hedistus</i> , <i>B. nevillei</i> , <i>Papilio xuthus</i> , <i>P. polytes</i> , <i>P. bianor</i> , <i>Parantica sita</i> , <i>P. melanuca</i> , <i>Tirumala septentrionis</i> , <i>Euploea mulciber</i>
<i>Eupatorium adenophorum</i>	<i>Papilio xuthus</i> , <i>Pieris brassicae</i> , <i>Pontia daphidice</i> , <i>Aporia agathou</i> , <i>Ypthima balda</i> , <i>Neptis hylas</i> , <i>Lampides boeticus</i> , <i>Potanthus pallida</i> , <i>Ochlodes subhyalina</i>
<i>Gynura segetum</i>	<i>Byasa urvilli</i> , <i>Papilio syfanius</i> , <i>Danaus grautia</i> , <i>Parantica melanuca</i> , <i>Tirumala septentrionis</i> , <i>Euploea mulciber</i> , <i>Acraea issoria</i>
<i>Cephalanoplos segetum</i>	<i>Papilio xuthus</i> , <i>Appias remedies</i> , <i>Danaus chrysippus</i> , <i>Chilodreua childreni</i> , <i>Vanessa cardui</i> , <i>V. indica</i>
<i>Taraxacum</i> sp.	<i>Pieris napi</i> , <i>P. melete</i> , <i>P. rapae</i> , <i>Ypthima balda</i> , <i>Y. iris</i> , <i>Y. nikaea</i> , <i>Callerebia suvoia</i> , <i>Heliophorus brahma</i> , <i>Zizina otis</i> , <i>Celastrina oreas</i> , <i>Lampides boeticus</i>
<i>Crepis</i> sp. / <i>Youngia</i> sp.	<i>Zizina otis</i> , <i>Lampides boeticus</i> , <i>Tougeia ion</i>
Papilionaceae	
<i>Vicia cracca</i>	<i>Papilio xuthus</i> , <i>Colias erate</i> , <i>C. fieldii</i> , <i>Pieris rapae</i> , <i>Lampides boeticus</i>
<i>Trifolium repens</i>	<i>Ypthima sacra</i> , <i>Zizina otis</i> , <i>Tougeia ion</i>
Rosaceae	
<i>Potentilla fulgens</i>	<i>Ypthima balda</i> , <i>Y. iris</i> , <i>Zizina otis</i> , <i>Celastrina oreas</i> , <i>Lampides boeticus</i> , <i>Potanthus pallida</i> , <i>Carterocephalus alcinoides</i> , <i>Ochlodes subhyalina</i> , <i>Pyrgus maculatus</i>
<i>Pyracantha fortuneana</i>	<i>Aporia agathou</i> , <i>Aglais urticae</i> , <i>Heliophorus brahma</i> , <i>Ahlbergia chalcidis</i> , <i>Celastrina oreas</i>
<i>Spiraea martinii</i>	<i>Ixias pyrene</i> , <i>Gonepteryx amantha</i> , <i>Syubrenthia hypselis</i>
Nyctaginaceae	
<i>Bougainvillea glabra</i>	<i>Papilio syfanius</i> , <i>P. bianor</i> , <i>P. polytes</i> , <i>P. xuthus</i>
Brassicaceae	
<i>Brassica campestris</i>	<i>Colias erate</i> , <i>C. fieldii</i> , <i>Pieris napi</i> , <i>P. melete</i> , <i>P. rapae</i> , <i>Eurema hecabe</i> , <i>Heliophorus brahma</i>
<i>Raphanus sativus</i>	<i>Colias erate</i> , <i>C. fieldii</i> , <i>Pieris rapae</i> , <i>Heliophorus brahma</i>
Malvaceae	
<i>Hibiscus mutabilis</i>	<i>Byasa hedistus</i> , <i>Papilio bianor</i> , <i>P. syfanius</i>
Ericaceae	
<i>Rhododendron</i> sp.	<i>Dodona durga</i> , <i>Heliophorus brahma</i> , <i>Ahlbergia chalcidis</i>
<i>Piris formosa</i>	<i>Dodona durga</i> , <i>Heliophorus brahma</i> , <i>Ahlbergia chalcidis</i>

working time (Fig. 5) provides a curve of sampling effect during the fieldwork (Raguso & Gloster, 1993). Species number increased sharply right after the initiation of this survey and slowed down afterwards, finally reaching an asymptote.

The taxonomic and faunal compositions documented illustrate the general faunal characteristics of the butterflies on Xishan Hill. Compared with previous records, more swallowtails and danaines were collected with fewer pierids, nymphalines, and riodinids. Two reasons for this phenomenon are possible: 1) recent butterfly manuals recognizing more species that now occur in Yunnan than earlier (Lee, 1995; Huang, 1987; Chou, 1994) and/or 2) tourist development extended the walking trails so more areas

could be surveyed than before. These species include: *Byasa hedistus*, which is similar to *B. polyeuctes* except an extra white spot on hind wing (Wu, 2001; Chou, 1998), *Papilio syfanius*, *P. protenor*, *P. machaon*, *P. helenus*, *Graphium cloathus*, *Catopsilia promona*, *Appias remedies*, *Hebomoia glaucippe*, and *Tirumala septentrionis*.

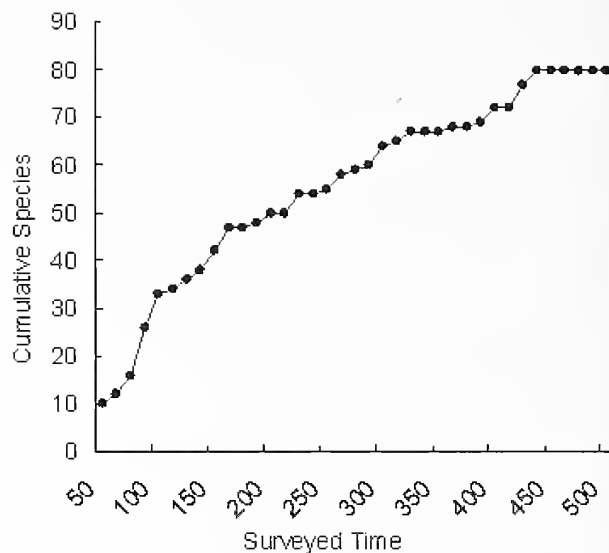
Eight species on the survey checklist are listed on the "China Species Red List (IUCN List)," with categories of NT and VU. During the survey, all eight species were abundant on the hill within their preferred habitats. The major reason they had been listed was their limited distributional ranges: *Ypthima iris* and *Y. dromon* are the only two endemic (to Yunnan) species on Xishan Hill, *Y. sakra* and *Y. nikaea* are distributed only in Yunnan and some adjacent

**Table 5.** Species collected or observed on non-floral materials.

Butterfly species	Attractans			
	Mud	Feces	Fruits	Other
<i>Byasa polyeuctes</i>				X <sup>2</sup>
<i>Papilio bianor</i>	X			X <sup>2</sup>
<i>Pontia daplidice</i>	X			
<i>Delias belladonna</i>	X			
<i>Lethe andersoni</i>			X	
<i>Lethe durga</i>	X		X	
<i>Lethe verma</i>	X		X	X <sup>1</sup>
<i>Neope yama</i>	X	X	X	X <sup>1</sup>
<i>Callerebia surioia</i>	X	X		X <sup>1</sup>
<i>Ypthima zodia</i>	X	X		X <sup>1</sup>
<i>Ypthima medusa</i>	X	X		X <sup>1</sup>
<i>Vanessa cardui</i>	X		X	X <sup>3</sup>
<i>Vanessa indica</i>	X	X	X	X <sup>1,3</sup>
<i>Aglais urticae</i>				X <sup>1</sup>
<i>Issoria lathonia</i>	X			
<i>Neptis hylas</i>	X			
<i>Junonia orithya</i>	X		X	
<i>Kaniska canace</i>	X		X	
<i>Acraea issoria</i>	X			
<i>Dodona durga</i>	X			X <sup>1</sup>
<i>Dodona onida</i>	X			
<i>Heliophorus brahma</i>	X			X <sup>1</sup>
<i>Zizina otis</i>	X	X		
<i>Ahlbergia chalcidius</i>	X			
<i>Lampides boeticus</i>	X			
<i>Celastrina oreas</i>	X	X		
<i>Carterocephalus alcinoide</i>	X			
<i>Pelopidas agna</i>	X			
<i>Lobocla proxima</i>	X			

Other objects including: 1. organic wastes dumped by tourists (food and fruit skin), 2. water, 3. tree fluid.

Asian countries (Sikkim, Bhutan, Nepal, and India). *Byasa hedistus* lives only in Yunnan and Fujian Province according to existing records. *Lethe andersoni* occurs only in Yunnan and Sichuan. *Lobocla proxima* is also found only in Yunnan and Sichuan Province. *Hebomoia glauccipe* has a wider occurrence, but illegal collecting has threatened the species (Wang and Xie, 2005). Five species of eight are Chinese endemics. All of them live in a very limited range within Chinese territory, resulting in compressed habitats that are vulnerable

**Figure 5.** Cumulative species numbers during the survey.

to human and natural disturbance. These species need protection with further knowledge about their biology and ecology needed. Under any circumstance, future conservation must focus on habitat protection (Kondla *et al.*, 1999).

Distinctive adult active periods were observed, with a clear gap between spring and summer generations. The reason for the phenomenon is that the spring generation's adults went through courtship, mating, and reproduction in the late spring or early summer and afterwards their numbers declined. Time is necessary for the next generation to develop and thus fewer adults were seen than in the prior period. After May, the summer generation adults emerged and numbers recovered. Some groups did not show evident gaps because of their large populations and generation overlap. The peaks of adult active periods are from mid March to May, then late June to early October.

Strong habitat affinities were demonstrated by the survey. Type 2 and 5 habitats are the most favored as a result of high plant diversity. Dense forests have high plant diversity, but insufficient sunlight reduces butterfly abundance. Farmland provides good nectar resources while monocultural plantations decrease butterfly abundance significantly, especially nymphalines, (Bobo *et al.*, 2006). Patches of farmland provide agricultural plants that host *Pieris spp.* and *Colias spp.*, are thus man-made habitats for these species.

Feeding habits were indicated by surveying preferred nectar plants and non-floral attractants.

Among plants, Asteraceae are most favored, but various butterflies visit different species of nectar source plants. This phenomenon implies an obligate relationship between butterflies and plants, supporting the viewpoint of previous behavior research. Butterflies are thus able to select nectar source plants instead of being opportunists when visiting flowers for food (Bhuyan *et al.*, 1999). Among non-floral attractants, mud is preferred, with most attracted butterflies taking water and mineral salts from there (Preston-Mafham & Rod, 1988; Lee & Zhu, 1996). Rotting fruits and other organic matter were the second favored attractants; the organic matter produced providing nutrition. Feces were only used by a few satyrines and nymphalines.

Taken together, the butterflies on Xishan Hill are a representative community of the Yunnan butterfly fauna. It is hoped that this survey will provide a benchmark for the future research and conservation.

#### ACKNOWLEDGEMENTS

I sincerely thank Cheng Hao from London University for great assistance during the field work, Yin Zhijian from School of Life Sciences, Yunnan University for assistance in plant specimen identification, and Chen Lin from the same department for providing excellent living photos of *Aporia agathon* and *Delias belladonna*. I also appreciate the efforts of several other personnel who provided generous assistance for this work, during and after the field survey course.

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#### APPENDIX 1: Checklist of collected butterflies and corresponding habitat types.

Species	Elevation	Fauna*	Habitat**
Papilionidae			
<i>Byasa hedistus</i> (Jordan)	2,270-2,340	O	2
<i>Byasa nevillei</i> (Wood-Mason)	2,180-2,340	O	2, 5, 7, 8
<i>Byasa polyeuctes</i> (Doubleday)	2,100-2,340	C	2, 5, 7, 8
<i>Papilio polytes</i> Linnaeus	2,280-2,340	C	2, 5, 8
<i>Papilio helenus</i> Linnaeus	2,050-2,270	O	2, 8
<i>Papilio protenor</i> Cramer	2,000-2,280	C	5
<i>Papilio xuthus</i> Linnaeus	1,900-2,340	C	2, 5
<i>Papilio bianor</i> Cramer	1,900-2,340	C	5, 8
<i>Papilio syfanius</i> Oberthür	2,280-2,340	O	2, 5
<i>Graphium cloanthus</i> (Westwood)	1,900-2,170	C	2, 5, 7, 8

Species	Elevation	Fauna*	Habitat**
<b>Pieridae</b>			
<i>Colias erate</i> Esper	2,010-2,340	C	4, 5
<i>Colias fieldii</i> Ménétriès	2,010-2,340	C	4, 5, 8
<i>Catopsilia pomona</i> (Fabricius)	1,900-2,340	O	2
<i>Eucema lacta</i> (Boisduval)	1,900-2,340	C	4, 5
<i>Eucema hecabe</i> (Linnaeus)	1,900-2,340	C	2, 5
<i>Gonepteryx amintha</i> Blanchard	2,170-2,340	C	2, 4, 5
<i>Gonepteryx rhamni</i> (Linnaeus)	2,030-2,220	C	2, 4
<i>Ixias pyrene</i> (Linnaeus)	1,900-2,190	O	5
<i>Delias belladonna</i> (Fabricius)	2,280-2,340	C	2, 7, 8
<i>Appias remedios</i> Schröder et Treadaway	2,300	O	4, 5
<i>Pieris brassicae</i> (Linnaeus)	1,900-2,340	P	2, 5
<i>Pieris melete</i> Ménétriès	1,900-2,340	C	4, 5
<i>Pieris rapae</i> (Linnaeus)	1,900-2,340	C	4, 5
<i>Pieris napi</i> (Linnaeus)	1,900-2,340	P	4, 5
<i>Aporia agathon</i> (Gray)	2,170-2,290	O	4, 5
<i>Pontia daplidice</i> (Linnaeus)	2,170-2,340	C	4, 5
<i>Hebomoia glaucippe</i> (Linnaeus)	1,900-2,020	O	2, 5
<b>Damainae</b>			
<i>Danaus chrysippus</i> (Linnaeus)	2,300	C	5
<i>Danaus genutia</i> (Cramer)	2,170-2,300	O	2, 5
<i>Tirumala septentrionis</i> (Butler)	2,170-2,340	O	1, 2, 5
<i>Parantica sita</i> (Kollar)	2,000-2,340	C	5
<i>Parantica melanea</i> (Cramer)	2,000-2,340	O	2, 5
<i>Euploea mulciber</i> (Cramer)	2,280-2,340	O	2
<b>Satyrinae</b>			
<i>Melanitis leda</i> (Linnaeus)	1,900-2,120	C	1, 2, 5, 9
<i>Lethe andersoni</i> (Atkinson)	2,000-2,110	O	1, 2, 9
<i>Lethe dura</i> (Marchall)	2,230	O	5, 6, 9
<i>Lethe verma</i> (Kollar)	1,900-2,270	O	5, 9
<i>Neope yama</i> (Moore)	2,220	C	2, 5, 9
<i>Ypthima balda</i> (Fabricius)	2,170-2,340	C	2, 5, 9
<i>Ypthima iris</i> Leech	2,170-2,340	E	2, 5, 9
<i>Ypthima dromon</i> Oberthür	2,200-2,300	E	2, 5, 9
<i>Ypthima nikaea</i> Moore	2,170	O	2, 5, 9
<i>Ypthima sakya</i> Moore	2,170-2,340	O	1, 9
<i>Ypthima zodia</i> Butler	2,170-2,340	O	2, 9
<i>Ypthima medusa</i> Leech	2,170-2,340	O	1, 9
<i>Callerebia suvoia</i> Tytler	2,170-2,340	O	2, 5, 9
<b>Nymphalinae</b>			
<i>Cethosia biblis</i> (Drury)	2,260	O	5
<i>Vanessa cardui</i> (Linnaeus)	2,100-2,340	C	2, 3, 5, 8
<i>Vanessa indica</i> (Herbst)	2,100-2,340	C	2, 3, 5, 8

Species	Elevation	Fauna*	Habitat**
<i>Ariadne ariadne</i> (Linnaeus)	2,200-2,250	C	2, 3, 5, 6
<i>Kaniska canace</i> (Linnaeus)	2,250	C	2, 3, 4, 5, 6
<i>Aglais urticae</i> (Linnaeus)	2,180-2,340	P	2, 4
<i>Junonia orithya</i> (Linnaeus)	2,130-2,260	C	5, 6
<i>Junonia hierta</i> (Fabricius)	2,120-2,300	O	5, 6
<i>Symbrethia hypselis</i> (Godart)	1,980-2,000	O	2
<i>Phalanta phalantha</i> (Drury)	2,230-2,300	O	2, 4, 5
<i>Issoria lathonia</i> (Linnaeus)	1,900-2,300	C	2, 5
<i>Argyreus hyperbius</i> (Linnaeus)	2,170-2,340	C	1, 2, 5
<i>Chlidreia childreni</i> (Gray)	2,170-2,340	C	2
<i>Melitaea yuenty</i> Oberthür	2,030-2,340	O	2
<i>Neptis hylas</i> (Linnaeus)	2,170-2,300	O	2, 3, 5
<i>Athyma opalina</i> (Kollar)	2,300	O	2
<i>Calinaga buddha</i> Moore	2,190-2,340	O	2
Acraeinae			
<i>Acraea issoria</i> (Hübner)	2,240-2,300	O	2, 5
Riodinidae			
<i>Dodona durga</i> (Kollar)	2,130-2,340	O	2, 5, 9
<i>Dodona outida</i> Moore	1,900-2,340	O	1, 2, 5, 8, 9
Lycaenidae			
<i>Lampides boeticus</i> (Linnaeus)	1,900-2,340	C	1, 2, 4, 5, 8
<i>Celastrina oreas</i> (Leech)	1,900-2,340	O	2, 4, 5, 6, 7
<i>Zizina otis</i> (Fabricius)	2,170-2,340	O	6
<i>Heliophorus brahma</i> Moore	2,010-2,340	O	3, 6
<i>Tongeia ion</i> (Leech)	2,180	C	2, 5
<i>Alibergia chalcidis</i> (Leech)	2,170-2,300	O	4, 5
<i>Jamides bochus</i> Cramer	2,300	O	2
Hesperiidae			
<i>Chaospes benjaminii</i> (Guérin-Ménéville)	2,130	O	8
<i>Potanthus pallida</i> (Evans)	2,290-2,340	O	2
<i>Carterocephalus alcinoide</i> Lee	2,100-2,340	P	5
<i>Pelopidas agna</i> (Moore)	2,250	O	8
<i>Lobocta proxima</i> (Leech)	2,300	O	1, 2, 3
<i>Ochlodes subhyalina</i> (Bremer et Grey)	2,180-2,340	C	1, 2
<i>Pygus maculatus</i> (Bremer et Grey)	2,180	P	5

\* The letters in the **Fauna** column represent one of four butterfly fauna areas: **O**: Oriental Region, **P**: Palearctic Region, **C**: cosmopolitan, **E**: endemic to Yunnan.

\*\* The numbers in the **Habitat** column represent the nine habitat types classified in this study.

# A newly observed form of symbiotic relationship between Reverdin's blue *Lycaeides argyrognomon praeterinsularis* (Verity), (Lycaenidae) and *Camponotus japonicus* Mayr (Formicidae)

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**Abstract.** Observations of an individual larva of Reverdin's blue named O-I, and its tending ants were made in the grassland at the foot of Mt. Fuji, Japan between 29 VIII to 1 X in 2003. During its 3rd to 4th instars, O-I larva was almost entirely protected from natural enemies by *Camponotus japonicus* Primary Tending Ants (PTAs) and Secondary Tending Ants (STAs). Prior to pupation, O-I entered a *C. japonicus* nest hole with a PTA and three unmarked ants. Many *C. japonicus* individuals, including the same PTAs and some STAs from the larval stage, as well as newly attending STAs, alternatively accompanied the pupa until emergence. This is a new form of symbiotic relationship between Reverdin's blue and *C. japonicus*. In the relationship characterized by what we term "loyalty," a specific individual of Reverdin's blue was tended by one or several PTAs, and some STAs, from the 2nd instar to adulthood.

**Key words:** facultative or obligate ant-association, Reverdin's blue *Lycaeides argyrognomon*, *Camponotus japonicus*, new form of symbiotic relationship, 'loyalty' system.

## INTRODUCTION AND METHODS

The study area is situated at 35° 26'N 138° 49'E, at 1020 m altitude and extending horizontally 11.6 km northeast from the summit of Mt. Fuji (Fig. 1). The surrounding area is part of the North Fuji training ground for Japan's Self-Defense Force. The landscape is a savannah of grassland (*Miscanthus sinensis*) with patchily distributed pine forests (*Pinus densiflora*) or shrubs (*Salix integra*).

The survey was carried out from 12 VII to 26 X in 2003 within an area of 14 m<sup>2</sup>, including an isolated colony of the *Indigofera pseudotinctoria* (Fig. 2). Total observation time was 7652 minutes. The time spent observing the Reverdin's blue individual, O-I was 6399 minutes, extending over 27 days from 25 VIII to 1 X. Table 1 summarizes the data taken over 30 minute-long observation periods from 29 VIII to 1 X (total 5077 minutes).

We marked the butterfly larva and tending *C. japonicus* ants with colored felt-tipped pen in order to distinguish them individually. The marking seemed not to disturb O-

I larva or tending ants because the larva quickly resumed its usual activities and the ants returned to tending O-I after cleaning their bodies to remove the new scent. After marking, appeared the liquid to quickly evaporate, leaving only dry marks on the subjects.

Reverdin's blue larvae have a DNO (Dorsal nectary organ) in the 7th segment. This study was conducted on the supposition that ants were attracted to secretions from the DNO's. We used video and digital cameras at a distance so as not to disturb the larva and the ants.

We mainly recorded behavior of individual tending ants and the time spent engaged in these behaviors and the responses of O-I being tapped by the tending ants' antennae.

On 23 IX, when I picked up a stone attached to the O-I pupa in its pupal stage, the attending ant cut the girdle yarn of the pupa. I bonded the end of the abdomen of O-I pupa to the attached rock and made girdle yarn with Cemedine glue. These treatments may have affected the time spent by O-I emerging from its pupal case.

## RESULTS

Table 1 summarizes the events for O-I (marked



**Table 1.** The individual changes and the percentage of ants tending to Reverdin's blue O-1 from 2nd instar to adulthood. PTA (STA) indicates Primary (Secondary) Tending Ant and 1-7 numbers indicate individuals. Cjs or Fjs indicate ant individuals of *Camponotus japonicus* or *Formica japonica* not individually marked. Percentages in each block illustrate the proportion of daily observation time each ant individual tended O-1. 'None' indicates the percentage of the time no ants tended O-1.

Stage of Reverdin's blue	Larva (2nd)	Larva (3rd)	Larva (4th)	Larva (4th)	Larva (4th)	Larva (4th)	Larva (4th)	Larva (4th)	Larva (4th)	Pupa	Pupa	Pupa	Pupa	Pupa	Pupa	Pupa	Pupa	Pupa	Pupa	Adult	Adult	Total (days)
Individual/Date	Aug 29	Sep 1	Sep 4	Sep 5	Sep 6	Sep 7	Sep 10	Sep 13	Sep 15	Sep 16	Sep 18	Sep 19	Sep 20	Sep 22	Sep 26	Sep 27	Sep 28	Sep 30	Oct 1	Observed/Total (days)		
PTA-1	69,6 %	xDied																			1/19	
PTA-2		88,5 %			29,0 %	78,6 %			0,5 %			0,7 %	0,6 %			7,6 %				25,4 %	15/19	
PTA-3					92,5 %	81,2 %															6/19	
STA-1	8,5 %	8,3 %																			4/19	
STA-2	13,5 %	0,1 %																			2/19	
STA-3																					6/19	
STA-4																					4/19	
STA-5																					6/19	
STA-6																					2/19	
STA-7																					5/19	
Cjs	1,3 %																				7/19	
Fjs	2,3 %	0,1 %																			2/19	
None	11,6 %	3,1 %			0,2 %	0,2 %															Total minutes	
Observation time (minutes)	512	337	55	78	407	810	45	30	536	41	40	587	476	60	48	531	37	312	135		5077	

with an orange spot from the 2nd through 4th instars) and the three PTAs and seven STAs of *C. japonicus* attending from the 2nd instar until the emergence of the butterfly.

During the 2nd instar, on 29 VIII, PTA-1 dominated attendance (present 69.6 % of the time; 63% of the time solely, 6.6 % of the time with STAs). During the 3rd instar on 1 IX, PTA-1 died and was carried off by a *Formica japonica* ant to its nest. O-1 was then attended by a new ant, PTA-2, a nest mate of PTA-1's. On this day PTA-2 dominated attendance of O-1 (88.5% of the time). During the 2nd to 3rd instars, a few unmarked *C. japonicus* or *F. japonica* ants tried to attend O-1 larva for short time intervals in the absence of PTA-1 or PTA-2.

From 4 to 7 IX, PTA-2 and PTA-3 wholly tended the 4th instar O-1. During the periods when only one ant was present either, PTA-2 or PTA-3, that individual was observed to tap the posterior part of O-1 larva near the DNO. When both attended together, they tapped different parts of O-1: PTA-3 the front part and PTA-2 the rear part near the DNO (Fig. 3-A), respectively. As the total time PTA-2 spent in attendance around the DNO was longer than that spent by PTA-3, PTA-2 took precedence over PTA-3. During the observation period, the time that no ant attended O-1 decreased from 12% in the 2nd instar to 3% in the 3rd and then to 0.2% in the 4th (Table 1, 29 VIII to 7 IX). O-1 was almost entirely protected from natural enemies during the period of 3rd to 4th instars by *C. japonicus*.

Because O-1 could not be found on the host plant on 10 IX, a stone (ca. 5 cm radius) was lifted near the host plants. Subsequently O-1 was found under the stone with an unmarked ant. Instead, O-1 was in a "room" formed by small pebbles; PTA-2 and two unmarked ants were there. O-1 larva then started to crawl under another small stone (ca. 1 cm in radius situated at the entrance of a *C. japonicus* nest hole) with PTA-2 and the three unmarked ants (Fig. 3-B). PTA-2 was searching and carrying a small pebble (2-3 mm in radius) from the original "room" to the nest hole occupied by O-1 larva (indicated by yellow arrows in Fig. 3-B), while other unmarked ants carried away many small pebbles surrounding O-1 larva. O-1 changed to pre-pupa the next day and pupated three days later.

The time ants spent under the stone during the pupal period was assumed to be the same as time spent tending to the O-1 pupa. That of PTA-2 turned out to be 0.5-0.7% of the total observed time (five to six minutes) for the six days following pupation, drastically less than that the time spent during the larval stage (Table 1). Table 1 shows that many individuals, including the same PTAs and STAs from

the larval stage and newly attending STAs, took turns tending the pupa. During the three days before butterfly emergence, PTA-2 spent much more time (7.6% of the total) under the stone and more than seven ants tended to the O-1 pupa.

O-1 began to emerge at 14:08 on 30 IX; 190 minutes later PTA-2 approached the emerging O-1 imago and began tapping the head and body with its antennae, and continued to do this for ten minutes until O-1 had partially extracted itself from the pupal case (Fig. 3-C).

PTA-2 then left the adult female O-1 without attacking (Fig. 3-D). Subsequently STA-7, which had attended the O-1 pupa, approached the emerged adult as it was hanging from a grass blade (about three cm height from the ground) and gently tapped it for about an hour (Fig. 3-E). During this time, PTA-2 tried to remove O-1's pupal case.

When the adult fell to the ground, PTA-2 followed. After the O-1 adult climbed up another grass blade, PTA-2 continued to walk on the ground for the remaining period of observation (80 mins) within about a meter radius of the grass blade but without climbing it. The observations of 30 IX are described in the Appendix. On 1 X, following emergence, we found the O-1 adult on the ground, having failed to expand her wings. STA-5, which had attended the O-1 pupa, was tapping gently on the O-1 adult with its antennae (9:30; Fig. 3-F). PTA-2 spent 25.4 % of 135 minutes removing O-1's pupal case.

## DISCUSSION

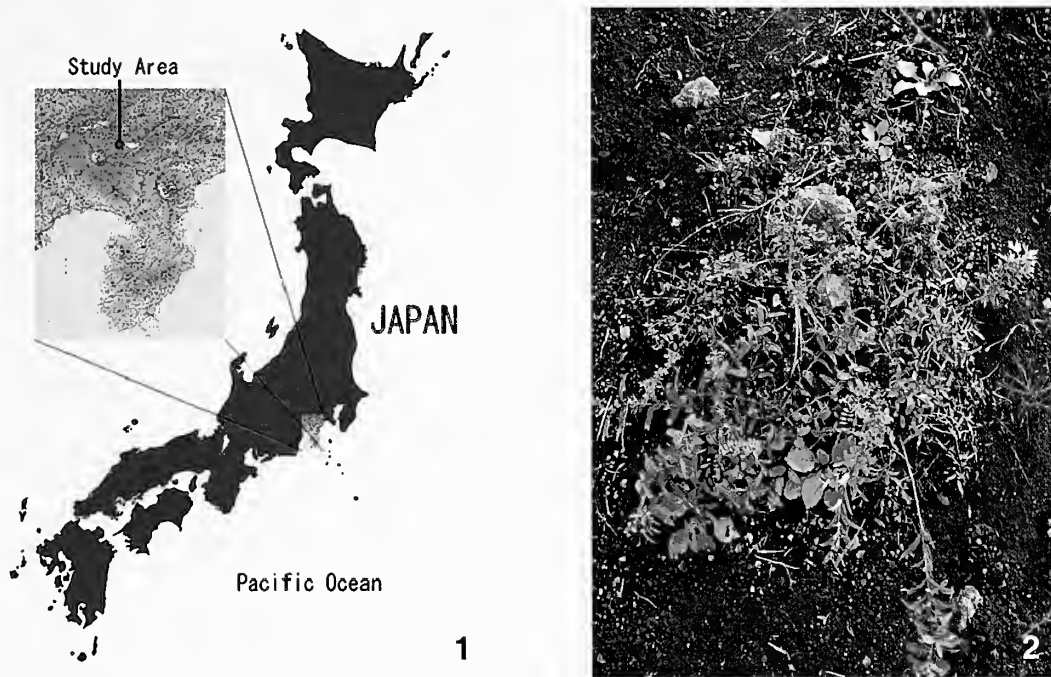
Mutualism is a successful adaptive strategy for butterflies (Hölldobler & Wilson, 1990). In Lycaenidae, with more than 6000 species worldwide, larvae of the majority of species studied maintain some association with ants at least during later stages of development (Fiedler, 2001).

Lycaenid-ant interactions have been classified with two types of ant-association: obligate, meaning larvae are dependent on ants for survival; or facultative, meaning larvae do not require attendant ants for survival (Bronstein, 1994; Osborn & Jaffe, 1997; Pierce *et al.*, 2002; Heath & Claassens, 2003).

Obligate myrmecophiles were classified further into subgroups obligate mutualist and obligate parasite (Fiedler, 2001), believed to be the result of chemical mimicry (Akino *et al.*, 1999; Thomas & Settle, 2004; Als *et al.*, 2004).

Reverdin's blue is a facultative species because it can be reared from egg to adult without any ants in captivity.

We do not know of any paper on symbiotic



Figures 1-2. 1. Study area. 2. Study site



**Figure 3.** The "loyalty" system in the newly discovered symbiotic relationship between Reverdin's blue and *Camponotus japonicus*. **A:** Two Primary Tending Ants (PTA-2, left and PTA-3, right) tending to larva O-1 (in 4th instar). **B:** Movement of the larva O-1 from the original pupation room (left arrow) to a new one (right arrow) at the entrance of ant nest with PTA-2 and three unmarked *Camponotus* ants. **C:** Tending behavior of PTA-2 toward the emerging pupa of O-1. **D:** Emerged imago in process of being tapped by PTA-2. **E:** Tapping behavior of Secondary Tending Ant (STA-7) aimed at hanging O-1 adult. **F:** Tapping behavior of STA-5 aimed at O-1 adult on morning following emergence (All photos taken by Watanabe).

behaviors, whether obligate or facultative, that has individually identified a butterfly and its tending ants. This paper has focused on individual behavior in the symbiotic relationship between the butterfly and its tending *Camponotus* ants during the period from larva to adult in nature.

Reverdin's blue had been previously reported to pupate on the larval host plant by using leaves to make its own nest (Fukuda *et al.*, 1984). In our study the last instar larva enters the ant's nest hole by its own effort, although accompanied by PTAs and STAs, to pupate there. Over forty Reverdin's blue pupae were found in or near ants' nest holes in 2004 and 2005 (unpublished data).

Our study also shows PTAs and STAs of *C. japonicus* tend Reverdin's blue's pupae until emergence. In our case of O-1, the tending *C. japonicus* concentrated on limited sections of the surface at the rear of the head and the abdomen of the O-1 pupa. Moreover, O-1 attracted at least nine individuals of the same colony to its nest throughout the pupal stage (Table 1).

In many myrmecophilous species, emerging adults are often killed if they fail to escape (Pierce *et al.*, 2002). So why was the emerged adult O-1, not attacked by its tending PTA, STAs, or other resident ants even when it took about ten minutes to emerge from the pupal case failed to expand its wings for over 2 hours.

*C. japonicus* PTAs thus appear to display a form of "loyalty" toward Reverdin's blue across all stages from larva to adult. This is a newly identified case of symbiotic relationship.

These observations concern just one individual of Reverdin's blue, O-1. However, the finding is supported by many other observations from 2004 to 2007 (unpublished data). During these four years of observations, the PTAs tending a particular specimen of Reverdin's blue sometimes turned over, but in small cases, specific PTAs or STAs of *C. japonicus* continuously tended one specimen as it developed from the 2nd instar to the pupal stage. The summary evidence clearly supports symbiotic "loyalty" by *C. japonicus* toward Reverdin's blue.

Reverdin's blue may have similar symbiotic relationships with at least four species of tending ants, *C. japonicus*, *F. japonica*, *F. yessensis*, and *Lasius japonicus* (unpublished data 2004-2005).

As symbiosis between butterfly and ants is an important interspecific interaction of ants with Lycaenids (Fiedler, 1998 and 2001; Pierce *et al.*, 2002; Heath & Claassens, 2003) and are characterized by a high degree of ecological opportunism and flexibility in associating with ants (Fiedler, 2001), the observed individual symbiosis described here may be

relatively common among other species pairs. Further observations and experiments will be conducted to better understand this symbiosis, particularly with endangered Lycaenid butterfly species. The relationship could be a key to conservation of endangered Lycaenid populations.

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## APPENDIX

**Detailed observations of emergence of O-1 on 30 IX. It was the first and longest observation of the Reverdin's blue made in the survey.**

- 
- |                 |  |
|-----------------|--|
| <b>14:08</b>    | It started emerging. A small crack on the pupa was observed with a camera with a close-up lens.  |
| <b>15:14</b>    | The crack got larger; it could be seen with the naked eye. The ants carried small pebbles around the pupa, and the stone with the pupa attached was repositioned to face us.   |
| <b>17:17</b>    | PTA-2 approached the emerging pupa and tapped on the body of both the pupa and the adult with its antennae (Fig.3-A). This behavior continued to 17:27.  |
| <b>17:27</b>    | The female O-1 adult emerged from the pupa (Fig.3-B). PTA-2 attended O-1 as it walked up the slope of the nest, tapping it once with its antennae. PTA-2 did not attacked to O-1 walking up slowly in front of PTA-2.                        |
| <b>17:30</b>    | As O-1 hung from the top of a blade of grass (about 3cm high), STA-7 approached O-1 and began tapping the body with her antennae (Fig.3-C). This behavior continued until 18:29, as PTA-2 tried to take off the shell of the pupa (Fig.3-D). |
| <b>18:29</b>    | PTA-2 approached O-1 and came into contact with STA-7.   |
| <b>18:42</b>    | When O-1 moved to a higher point (about 5cm from the ground), STA-7 disappeared after contacting PTA-2. O-1 remained still while PTA-2 wandered around O-1 or tried to remove the shell of the pupa. PTA-2 never tried to climb up to O-1.   |
| <b>19:30:48</b> | O-1 moved to another point (about 10 cm high) and continued to hang on. When Watanabe tried to mark the legs of O-1 with a blue felt-tipped pen, O-1 moved its unstretched wings.  |
| <b>19:30:58</b> | When Watanabe tried to mark O-1 again with the felt-tipped pen, O-1 dropped down to the ground. Just then, PTA-2, which had been taking off the shell of the pupa, approached O-1. PTA-2 looked for O-1 on the ground.                       |
| <b>19:32:21</b> | PTA-2 found O-1 walking on the ground and tapped on O-1 with its antennae. PTA-2 followed O-1 and induced O-1 to climb up to a higher point with its antennae-tapping.   |
| <b>19:40:30</b> | PTA-2 and O-1 separated from each other.   |
| <b>19:41:50</b> | O-1 climbed up the grass 10cm high from the ground and remained still. We observed O-1 and PTA-2 until 21:00. O-1 rested at the same point while PTA-2 was wandering on the ground around O-1 within about a one-meter radius.               |
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## NOTES

## Fabaceae, a new host plant family for *Hypanartia* and for the Neotropical Nymphalinae (Lepidoptera: Nymphalidae).

*Hypanartia* Hübner [1871] are medium-sized butterflies whose members are recognized by the orange, brown or reddish-brown color on the dorsal surface, angular wing shapes, and hindwing tails with variable length (DeVries, 1987; Willmott *et al.*, 2001). The genus contains 14 species, with the center of diversity in high Andean cloud forest habitats (Willmott *et al.*, 2001). The known larval host plants for *Hypanartia*, like other genera of Nymphalini, include mainly Urticaceae and Ulmaceae (see Beccaloni *et al.*, 2008; Nylin & Wahlberg, 2008), with a single record for Piperaceae (Alayo & Hernández, 1987).

*Hypanartia bella* (Fabricius, 1793) is a common and widespread species that occurs in several types of habitats in the Southern Peru to the northern Argentina, eastern and southeastern Brazil, Uruguay and Paraguay (D'Abrera, 1987; Willmott *et al.*, 2001). The immature stages are relatively well known and host plant records include *Celtis*, *Trema* (Ulmaceae), *Urtica*, *Phenax*, *Boehmeria* and *Parietaria* (Urticaceae) (Biezanko, 1949; Hayward, 1969; Toledo, 1973; Brown, 1992; Beccaloni *et al.*, 2008). This note is to record a new host plant family for *H. bella* that represents a new record for the Neotropical Nymphalinae. In addition, some aspects of oviposition and larval behavior on this new host plant are described and discussed.

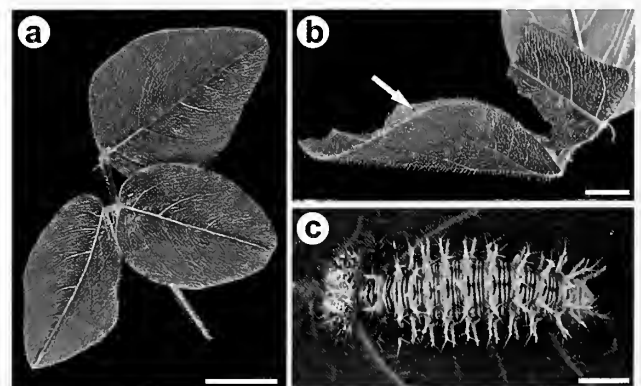
Field observations were conducted in three sites of Atlantic Forest in Rio Grande do Sul State, South Brazil: 1) Morro Santana (80 m a.s.l.), Porto Alegre (30°04'S, 51°07'W), in several opportunities between 2002-2005; 2) Barra do Ouro (450 m a.s.l.), Maquiné (29°30'S, 50°15'W), in October 2002; and 3) Floresta Nacional do Pinho (800 m a.s.l.), São Francisco de Paula (29°26'S, 50°34'W), in December 2006. The oviposition behavior was observed in the field, and the immature stages were collected and reared to confirm the viability of host plant in the larval development.

Eggs and larvae of *H. bella* were observed on *Desmodium uncinatum* (Jacq.) DC. (Fabaceae), a prostrate herb densely covered with hooked trichomes (Figs. A-B). Oviposition behavior on *D. uncinatum* was observed in two localities (Porto Alegre and São Francisco de Paula). Females of *H. bella* fly near to the vegetation and eventually land on potential plants (oviposition observed between 12:00-13:00 h). To find the appropriate host plant the female spends some

time inspecting (up to 3 min.). The butterfly can lay several eggs per plant, with eggs laid singly or in small groups of two or three. Eggs are placed on different plant parts, including new and old leaves, petioles and stems. The immature stages are similar to those described by Toledo (1973) from Argentina and from other localities in SE Brazil (AVLF unpublished). Eggs are light green, the larvae yellowish with large scoli in the last instar (Fig. C). All instars construct leaf shelters built as semi-rolled leaf held by silk (Fig. B).

The use of Fabaceae by a Nymphalinae species is striking. This is the first report of the plant family by a Neotropical Nymphalinae, but the use of Fabaceae has been reported rarely in *Vanessa cardui* (Linnaeus, 1758) and *Vanessa virginiensis* (Drury, 1773) in the Holarctic region (Scott, 1986; Tolman & Lewington, 1997).

*D. uncinatum* is a native plant in the Neotropics and can become invasive in some situations, infesting pastures, road edges, and waste land, mainly in southern and southeastern Brazil (Lorenzi, 2000). Thus, it is predictable that *H. bella* often encounters this plant species throughout its geographic distribution. However, the use of *D. uncinatum* by *H. bella* was confirmed only in these three localities in southern Brazil, suggesting that this new host plant use is a local phenomenon. The colonization of new host plants is



**Figure 1.** *Hypanartia bella* on *Desmodium uncinatum* host plant. **A**, leaves; **B**, detail of leaves, note the larval shelter (arrow); **C**, last instar in dorsal view. Bars = 1.5, 1.5, and 0.5 mm, respectively.

an important phenomenon in butterflies (Willmott & Freitas, 2006; Janz *et al.*, 2006). In Nymphalidae, recent studies have shown that the plasticity in host plants ranges may be related to diversification processes (Weingartner *et al.*, 2006; Nylin & Wahlberg, 2008). In this sense, *H. bella* may be a model for understanding the importance of local adaptation in the evolution of host plant use in Neotropical butterflies.

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## Duration of molt in a Neotropical butterfly (Lepidoptera: Nymphalidae)

In this note I present the results of an observational study on the length of molting in caterpillars of *Hypothyris ninonia daeta* (Boisduval, 1836), an ithomiine (Lepidoptera: Nymphalidae: Ithomiinae) butterfly of southeastern Brazil. To determine the proportion of time spent molting I measured the time caterpillars spend in molting relative to total development time. I was able to do this using a specific external marker (see below) that enabled me to recognize the start and the end of each molt period.

The species, hereafter referred to as *Hypothyris*, is a

medium-sized (forewing length 29-32 mm), relatively common butterfly inhabiting the Reserva Biológica do Poço D'Anta (RPA), a 277 ha forest fragment in Juiz de Fora, MG, Brazil (21°45'S, 43°20'W) (Costa, 2002).

*Hypothyris* has five larval instars that feed exclusively on *Solanum* (Solanaceae) species (Costa, 1999). Ovipositing females lay their eggs singly on the underside of hostplant leaves. Neonates are approximately 1.5-2 mm in length and are translucent white. Their color turns from white to greenish after feeding. However, since food consumption

stops during the molt process, and the larva partially evacuated its gut in preparation for molt, the distal end of the body changes coloration from a characteristic gray-green to translucent white. This color change of the last larval body segments thus provides a simple and reliable external marker that indicates the start of each larval molt, thereby facilitating the precise determination of the duration of each molt.

The color change mediated by gut contents does not occur in caterpillar species that have a pigmented or otherwise opaque body wall. For such cases, it is difficult or impossible to determine the start of molt process based upon visual inspection. Consequently, *Hypothyris* larvae provide an ideal subject for the study of molting behavior. For the pupal molt, color changes from gray-green to brownish and then to whitish. In all cases, shedding of the old head capsule marks the end of molt.

I collected *Hypothyris* immatures from a previously used study site at RPA (Costa, 1996) with all eggs and larvae between 21.IV (n = 14) and 1.V.1995 (n = 2). The 16 specimens were reared under semi-natural conditions, indoors, subjected to natural photoperiod and air temperature fluctuations, between 22.IV and 23.VI.1995 through adult emergence (8 ♀♀, 5 ♂♂). Each larva was reared individually in a glass jar with moist filter paper. Larvae were fed *Solanum cernuum* Vell., an abundant hostplant (Costa, 1999). Frass was removed with leaves and moisture were supplied as necessary.

The data for the study were from: (1) five immatures individuals (4 ♀♀: # B7, B8, B10, B12; 1 ♂: B5) reared from egg to adulthood (used to compute species-specific parameters); (2) four immatures individuals (B1, B2, B3, B4) that were collected as larva (three L3, one L5) and reared to adulthood; (3) two immatures individuals (B9, B11) reared from egg to adulthood but that molted to an extra sixth instar before pupation; and (4) two immatures individuals (P1, P2) collected as eggs on 1.V and that were reared to adulthood in different (plastic) containers. The other three immatures (B6, B13, B14) collected as eggs on 21.IV died during their second instar.

All caterpillars were examined by means of a magnifying lens 3-6 times daily for approximately 1-3 minutes each to determine the time spent during each larval instar during both growth (feeding) and molting (non-feeding) periods. This resulted in 139 surveys between 22.IV and 29.V.1995, when the last larva pupated. For each determination, I categorized caterpillar behavior as either "growth" (feeding, resting, moving around) or molting. I also noted activities such as mode and place of feeding, mode and place of resting, body aspect during molting,

etc. For computation, I assumed that all changes between growth and molting behavior occurred at the midpoint of the time interval between any two consecutive surveys. Larval size (body length to the nearest 0.5 mm) was measured at least once during each instar.

The climate at Juiz de Fora is characterized by a warm rainy summer and a cool dry winter. The average monthly temperature is 18.7°C, varying from 21.6°C (February) to 16.1°C (July). The diurnal range in air temperature greatly exceeded this average monthly change of only 5.5°C. On the other side, the monthly distribution of precipitation is very unequal throughout the year, varying from 272 mm (January) to 19 mm (July). Mean annual precipitation is ~1,500 mm (Costa, 1991).

To test whether the duration of the molt period is a function of the growth period of the same instar, I used linear regression analysis (least square). As a complement, I also used regression analysis to test if the time spent in each stage of development is a constant proportion of the total developmental time. Statistics (tests, symbols, and terminology) followed Sokal and Rohlf (1981)

Eleven of thirteen reared larvae had the usual five larval stages, but two caterpillars molted to an extra sixth instar before pupation. The latter two larvae were much smaller in body length (ca. 15 mm) when they underwent the extra instar. These exceptions are concordant with the hypothesis that there is a critical minimal length for a caterpillar prior to pupation (Nijhout, 1975; see also Esperk *et al.*, 2007).

Table 1 gives the average time in the growth stage of *Hypothyris* caterpillars increasing with successive

**Table 1.** The time duration of *Hypothyris* caterpillars during different instars (L1-L5) and corresponding molts. Values are means  $\pm$  SD from five larvae.

Phase (length, mm)	Duration $\pm$ SD (hours)
L1 (1.5-3.5)	73.31 $\pm$ 6.85
L1-L2 molt	14.45 $\pm$ 5.21
L2 (3.5-5.5)	118.75 $\pm$ 54.69
L2-L3 molt	21.14 $\pm$ 2.55
L3 (6.0-8.0)	119.11 $\pm$ 50.72
L3-L4 molt	20.65 $\pm$ 3.26
L4 (8.5-13.0)	116.51 $\pm$ 23.07
L4-L5 molt	28.03 $\pm$ 3.25
L5 (13.5-27.0)	169.84 $\pm$ 23.33
L5-pupa molt	36.93 $\pm$ 6.41



larval instars, changing from 73.31 hours  $\pm$  6.85 SD in L1 to 169.84 hours  $\pm$  23.33 SD in L5. In parallel, the average time spent in the molt stage also increased with larval instar, changing from 14.45 hours  $\pm$  5.21 SD (L1-L2 molt) to 36.93 hours  $\pm$  6.41 SD (L5-pupa molt, including prepupa). However, considering larvae B9 and B11, these values are higher: 212.53 hours  $\pm$  43.85 SD (L6) and 41.4 hours  $\pm$  11.58 SD (L6-pupal molt).

The duration of growth and molting periods of the same instar are related; longer feeding periods correspond to longer molting periods (linear regression analysis for data of Table 1:  $R^2 = 0.8544$ ;  $t = 4.19$ ;  $p < 0.05$ ). This relationship remains significant even including in the regression analysis data from all 13 caterpillars (Fig. 1).

The results of the regression analysis with data of Table 1 indicate that approximately 85% of the variation in the length of molting was explained by variation by duration of growth. The result appears relevant and more so considering that the sample included caterpillars from different instars growing simultaneously under a naturally fluctuating daily temperature regime.

In relative terms, the duration of molt periods varied from 14.7% (L3-L4 molt) to 19.4% (L4-L5 molt) of the total time that larva spent in each instar period (Table 1). However, the percentage of time spent by caterpillars during molting was not a function of the total duration (growth plus molting) of each instar (linear regression analysis:  $R^2 = 0.098$ ;  $t = 0.57$ ;  $p > 0.9$ ), as would be expected if molt duration were

a fixed proportion of instar length.

Like other ectotherms (e.g., Casey, 1993), the performance of *Hypothyris* caterpillars is temperature-sensitive and varies in different months of the year. For instance, studies on the performance of these caterpillars in the field have shown that the growth rate increases linearly with temperature (unpublished data). Thus, the results of this study, which were obtained during autumn when the number of immatures in the field is decreasing, may overestimate the values during warm seasons, spring and especially summer, when immature density is higher (Costa, 1991) and development is probably faster. I believe the results of this study show that molting and growing periods of *Hypothyris* caterpillars are correlated, so that larval growth rate can be reduced directly (i.e., low temperatures prolong molt period) or indirectly (i.e., low temperatures prolong growth period that implies in a molt period correspondently longer).

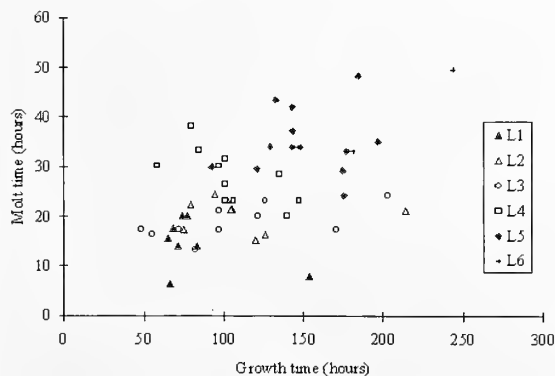
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**Figure 1.** Relationship between growth and molting periods of the same instar (from L1 to L5 plus two extra L6) for 13 *Hypothyris* caterpillars. The linear regression analysis for all these data also produced significant results ( $R^2 = 0.2708$ ;  $t = 4.52$ ;  $p < 0.001$ ). In this figure, seven of the original 57 points are coincident: two full triangles (L1), three empty circles (L3), and two empty quadrats (L4).



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## *Euselasia mys lara* (Stichel, 1919) (Lepidoptera: Riodinidae) a potential pest on *Eucalyptus* in Brazil?

*Eucalyptus* species have been used across large areas of reforestation in Brazil over the past 40 years (Zanuncio *et al.*, 1990). High yield from these reforestation result from widespread use of clones (Laranjeiro, 1994; Zanuncio *et al.*, 2001), but the genetic uniformity among clones increases vulnerability to insect pests (Zanuncio *et al.*, 2003). All the *Eucalyptus* leaf eating Lepidoptera in Brazil are native species generally using Myrtaceae (Holtz *et al.*, 2003a). The adaptation of native insects to *Eucalyptus* have been reported elsewhere: China, India, New Guinea and Sumatra (Ohmart & Edwards, 1991). In Brazil *Eupseudosoma aberrans* (Schaus, 1905) and *Eupseudosoma involuta* (Sepp, 1855) (Lepidoptera: Arctiidae), *Automeris sp.* (Walker) and *Eacles imperiales* (Walker, 1856) (Lepidoptera: Saturniidae), *Sabulodes caberata* (Guenée, 1857), *Thyriniteina arnobia* (Stoll, 1782) and *Oxydia vesulia* (Cramer, 1779) (Lepidoptera: Geometridae) are examples of insect adapting to *Eucalyptus* crops (Zanuncio *et al.*, 1998). *Mimallonia amilia* (Cramer, 1780) (Lepidoptera: Mimallonidae), originally a pest of *Myrciaria dubia* in the Amazon region (Zanuncio *et al.*, 2005), has been reported as a secondary pest of *Eucalyptus wrophylla* in the region of Três Marias, Minas Gerais State, Brazil (Pereira *et al.*, 2001).

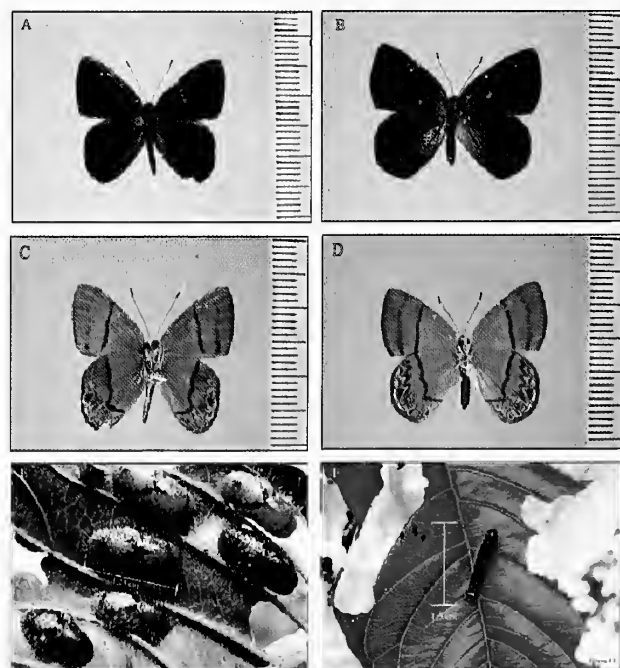
The genus *Euselasia* is distributed throughout the tropical region where it has great diversity, exemplified by 167 species named to date from Mexico to Bolivia, Argentina and Uruguay (Callaghan & Lamas, 2004), with 24 species found at one site in Ecuador (Murray, 2000). In Brazil, caterpillars of the *Euselasia* genus have been reported on *Psidium araca*, *Psidium guajava*, *Eugenia pitanga*, *Eugenia uniflora* and *Eucalyptus spp.* (Silva *et al.*, 1968). *Euselasia eucerus* (Hewitson, 1872) (erroneously reported as *Euselasia apisaon*) damaged 20.000 hectares of *Eucalyptus* forests in the Vale do Rio Doce and mining áreas in Minas Gerais State, Brazil (Moraes *et al.*, 1983). *Euselasia eucerus* (*Euselasia apisaon*) was found on *Eucalyptus cloeziana* plantations in the region of São Pedro dos Ferros, Minas Gerais State, Brazil (Zanuncio *et al.*, 1990). Eggs of *Euselasia hygenius* (Stoll, 1790) were collected on *Eucalyptus wrophylla* reforestation in the municipality of Aracruz, Espírito Santo State, Brazil (Zanuncio *et al.*, 1995).

Numerous larval colonies of a riodinid of all stages were observed from February to May 2006 on guava tree leaves (*Psidium guajava*) at the Federal University of Viçosa in Viçosa, Minas Gerais State, Brazil. Samples

of branches of trees with colonies were wrapped in white organza bags (20 x 30 cm) and the larvae allowed to pupate. The pupae were removed to a laboratory environment where they were maintained at  $25 \pm 2^\circ\text{C}$ ,  $70 \pm 5\%$  RH with 12 hour L/D. The resultant adults were subsequently determined by Olaf Mielke as *Euselasia mys lara* (Stichel, 1919). Both sexes of adults are given in figures 1 to 4.

The larvae are gregarious, moving about in single lines and remaining on the abaxial leaf surface or walking on stems, leaves and branches of the guava tree when they are not feeding. During the first instar the larvae feed only on the leaf surfaces. The later instars consume entire leaves. The cephalic capsule is pale yellow and the body dark gray and with six longitudinal white stripes, four dorsal and two ventral. In the last instar they have pale yellow setae. Pupation occurs most frequently on the abaxial surface of leaves. The pupae are pale yellow with brown spots and many pale yellow hairs and do not display sexual

**Figure 1.** *Euselasia mys lara* (Lepidoptera: Riodinidae). Dorsal view of adult male (A); Dorsal view of adult female (B); ventral view of adult male (C); ventral view of adult female (D); pupa, bar= 1,25 cm (E) and caterpillar in the last stage, bar= 1,5 cm (F).



dimorphism.

On the other hand, *E. mys lara* adults show strong sexual dimorphism with the upperside of both wings of males being black with dark red spots that start close to the thorax and radiate to the wing edge. These spots are absent in females. The underside of the wings of both sexes are pale gray in color with 0.01 cm wide pale orange stripes that start from the anterior and continue to the posterior of the wings. The secondary wings have five black spots surrounded by white halos. The wings of the males of the species average a 3.0 cm wingspan and the females 2.6 cm. The head of both sexes present a white 'V' when viewed from the front, the abdomen is dorsally black and pale gray ventrally.

This is the first report of *E. mys lara* feeding upon guava, with the species not previously reported on any Myrtaceae, including *Eucalyptus*. Larvae of *E. mys lara* differ from those of *E. eucerus* (*E. apisaon*) in the latter having a last instar with a black head capsule, green coloring and pale setae on the legs (Zanuncio *et al.*, 1990). The related *E. hygenius* larvae has segments with two yellow dorsal spots, from which tufts of green setae arise. They also have three longitudinal stripes, one dorsal and two ventral (Zanuncio *et al.*, 1995). Pupae of *E. mys lara* also differ from those of *E. hygenius* that are a uniform yellow color, while those of *E. eucerus* (*E. apisaon*) are gray brown without hairs (Zanuncio *et al.*, 1990; Zanuncio *et al.*, 1995).

*E. eucerus* adults (*E. apisaon*) also showed sexual dimorphism: the male upperside wings are brick red colored with dark edges, the females being dark gray with some variants having three pair of white round spots in the middle of the primaries (Zanuncio *et al.*, 1990). By contrast, *E. hygenius* does not display sexual dimorphism, with upperside wings black in both sexes (Zanuncio *et al.*, 1995). These characters clearly distinguish the three species in both early stages and adults.

The abundance of species of the *Euselasia* genus in Brazil and reports of *E. eucerus* and *E. hygenius* feeding upon *Eucalyptus* implies that other species of the genus may damage plantations as a result of adaptive pressures across extensive reforestation areas of Brazil (Holtz *et al.*, 2003b). This has occurred with other Lepidoptera, including *Thyrineina arnobia* (Lepidoptera: Geometridae), considered the main leaf eating larva of *Eucalyptus* in Brazil (Cavalcante *et al.*, 2000; Santos *et al.*, 2000; Holtz *et al.*, 2003a; Oliveira *et al.*, 2005). Accordingly *E. mys lara* should be included in pest monitoring programs for *Eucalyptus* since the butterfly does occur in Minas Gerais State on a phylogenetically similar host, the guava. Additional studies are clearly called for regarding the *E. mys lara*

autecology and control methods.

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## Observations of late instar larva survival of *Cotesia* (Hymenoptera: Braconidae) parasitoid attack of *Euphydryas anicia cloudcrofti* (Lepidoptera: Nymphalidae).

Over the course of rearing a population of 100 *Euphydryas anicia cloudcrofti* (Ferris & Holland, 1980) (Lepidoptera: Nymphalidae) in captivity, an interesting observation emerged of a unique parasitoid-host interaction. The parasitoid infecting this population was identified as belonging to the genus *Cotesia* (Hymenoptera: Braconidae). Current molecular studies are under way to determine the exact identity of this parasitoid, which may represent a new species of *Cotesia*.

The first observation of *E. a. cloudcrofti* larvae attacked by a parasitoid came from three wild collected larvae in October of 2006. These larvae were in the third and fourth instars, and all of these larvae died shortly after the *Cotesia* larvae emerged to pupate. In the following spring, three post-diapause larvae (fifth and sixth instars) were able to survive after the *Cotesia* larvae emerged to pupate. These surviving larvae became very lethargic and refused to eat for several days, but then seemed to recover. Two of these larva proceeded to pupate, while the third died before pupation. Of the two larvae that immediately pupated, one emerged as a normal adult and the other displayed wing deformities. The same phenomenon was observed again with wild-caught larvae in 2007 (from a total population of 100 larvae), when the early instars died after parasitoid emergence but a single late instar larva survived the parasitoid attack.

Parasitoids are distinguished from parasites by the very fact that they cause the eventual death of the host (Godfray 1993; Borrer *et al.*, 1981; Ricklefs,

1979), but this observation of *E. a. cloudcrofti* survival, however, along with observations of Arctiid larva (*Platyprepia virginialis* (Boisduval)) surviving *Thelainia bryanti* emergence (English-Loeb *et al.*, 1990), may cause us to reconsider the relationship between parasitoids and parasites with their hosts. Perhaps it would be more appropriate to view this relationship as a continuum with at one end pure parasitoids cause certain host death; while at the other pure parasites cause certain host survival; and intermediate points along the continuum represent less certain host survival outcomes.

Although host survival of parasitoid attack may be rare, the fact that it occurs at all in Lepidoptera is biologically significant because it suggests that specific conditions exist that will permit a host to survive a normally fatal parasitoid attack.

Investigations to define conditions that permit host survival would be warranted. In this case the common feature between the *E. a. cloudcrofti* and *P. virginialis* observations is that they occurred in captive reared populations. It is possible that some condition of artificial rearing better enables a host to survive parasitoid attacks.

It is also quite possible that this phenomenon occurs at such low frequencies in the wild population that it has gone undetected. Ehrlich and Hanski (2004) noted *Cotesia* parasitizing checkerspot butterflies often display specialized behaviors that are not characteristic of their congeners. Host survival may be a result of this specialized *Cotesia* behavior, or it may be the result

of an evolutionary adaptation of *E. a. cloudercrofti* larvae to counter parasitoid attack.

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## BOOK REVIEWS

**Olethreutine moths of Australia (Lepidoptera: Tortricidae) by Marianne Horak, with contributions by Furumi Komai, 2006**

Monographs on Australian Lepidoptera, volume 10. CSIRO Publishing. 522 pages. AU\$ 160.

The family Tortricidae is one of the most diverse and economically relevant groups of microlepidoptera. The volume 10 of the prestigious series 'Insects of Australia' treats one of its main subfamilies: Olethreutinae.

The structure of the book is similar to previous issues of the series. After the introduction and a short but instructive chapter on material and methods, the book includes chapters devoted to phylogeny, morphology, biology, diversity and distribution. The core of the book—more than 400 pages—is devoted to the taxonomic revision of genera and species of the Australian fauna.

Even those familiar with the Lepidoptera will find the chapter on morphology extremely useful with accurately detailed information on the characters. The treatment of the characters is absolutely consistent throughout the book.

The phylogenetic analysis is divided into two parts as the matrix is presented in an appendix at the end of the book, which does not represent any problem for the reader. Prudently the author presents the cladogram as insufficiently conclusive to suggest changes to the higher classification of the group. The intriguing results deserve, however, some attention. The genus *Gatesclarkeana* and allies are returned to Olethreutini *s. str.* and not as a separate tribe Gatesclarkeanini. The tribe Bactrini is placed as a derived group and not as a rather primitive one. In addition, Bactrini—that is treated including *Endothenia*—represents a paraphyletic group with respect to *Lobesia*. This resurrects the classical discussion about the close relationship between *Bactra*, *Endothenia* and *Lobesia*. The definition of Enarmoniini (= Ancylini) is refined with new Australian material. This tribe is spread in the cladogram as polyphyletic, although the core of the group represents a consistent monophyletic clade in which *Ancylis* is placed in a relatively derived position. Thus Enarmoniini *s. str.* fits into Eucosmini that becomes a paraphyletic group. The monophyly of Grapholitini is not questioned and the whole tribe is represented in the analysis by the genus *Grapholita*. Although the reconstruction is based on the Australian fauna, this is one of the most challenging

phylogenetic analysis ever attempted for the subfamily and will be a reference for future work, specially in the molecular scenario.

A key to the Australian genera of Olethreutinae introduces the taxonomic part in which every genus is reviewed following a research paper structure. The volume reviews the 90 genera occurring in Australia, including twelve new genera. The specific treatment does not pretend to be exhaustive, but about 250 named and 200 unnamed species are treated, with 41 new combinations proposed. The natural connections between the Australian and the Oriental faunas are not overlooked, and 80 new combinations for non Australian species are proposed. The Grapholitini chapter is coauthored by Furumi Komai, the leading authority in the tribe, and Marianne Horak. This does not represent any detectable change in style or structure.

The book is profusely illustrated with nearly a thousand photographs including, when available, male and female genitalia, sclerite details, scanning electron microscope slides of the head, and wing pattern. Perhaps the inclusion of color printing for the wing patterns would have improved the detail but this would have demand to separate the wing patterns in plates and the option has been to include all the illustrations together within the text.

Few people are involved today in producing fine, detailed monographs. Although such work will ensure the availability of a comprehensive taxonomic knowledge for future generations, in a scientific scenario where rapid-impact outputs are given priority, broad revisionary work is vanishing. However, Marianne Horak's option was to devote an effort of nearly two decades to produce a single monograph of a difficult and puzzling taxonomic area full of obscure taxonomic identities and complex phylogenetic relationships. The challenge has been enormous. While this is a geographically restricted project, the fauna of Australia includes so many primitive and endemic taxa that the book must be regarded as a standard reference for anyone interested in tortricid research. Beyond this, the perfectionism that permeates the whole work places

it as a role model for systematic Lepidoptera research in all time and place.

Marianne Horak received the first J. O. Westwood Medal for excellence in insect taxonomy for her work with Olethreutine Moths of Australia. The Westwood Medal is a joint biennial award launched by the Royal Entomological Society and the Entomology Department of the Natural History Museum for the

best comprehensive taxonomic work published on a group of insects or related arthropods. Little can be added to this more than deserved award except congratulate the author and the publisher for this outstanding work.

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## A guide to Australian moths by Paul Zborowski and Ted Edwards, 2007

Paperback, 224 pages, ca. 400 color photos. CSIRO Publishing, Collingwood, Vic, Australia. AU\$39.95.

I'm mad as hell and wont take it any longer has become a common refrain in our ever more stressful world. Our participation in biodiversity studies seems to be slowly declining along with biodiversity itself. While the widespread use of lepidopterous imagery, especially in advertising and branding goes forward, studies do not. In fact the use of bioscience grows as PR and marketing tools. The public becomes a receptacle for spectacle. As purveyors of biodiversity we have been largely ignored in the scheme of things. We don't even know how many species of insects there are in greater New York, much less how they interrelate and respond to our world of here and now. The billions spent on a few spectacular events like finding ice on Mars or orbiting telescopes, although valid, are misplaced by cost benefit while voices in (and for) the wilderness, as E. O. Wilson, are barely audible. Of course we could start on the value of environment impact statements and what we aren't learning, but that will be a diatribe for another day.

So here comes as marvelous and well-produced book radiating the grandeur of moth variation in its overview of the moth fauna of Australia. Brilliantly illustrated, it should peak the curiosity of anyone with concerns for understanding life and the world around us. Not only the beauty of the creatures shown, but of their relationships both structural and biological that are succinctly described. I learned a lot from this piece from its elementary introduction on biology and role of moths to the descriptive section. The work is especially well organized and well written. The authors clearly were enthusiastic and involved.

There are about 20,000 known, with a projected 10,000 more unknown, species of moths in Australia. The 32 page introductory section gives and answers 14 basic questions on moth biology, covering their evolution and ecology, but framed in pragmatism for the lay reader. What use are moths, why do they

have so many shapes and colors, and of what use are they? The question "have any moths become extinct," leads off with the seminal answer that "No Australian moth is considered extinct but this is because so little is known about the distribution, ecology and identification of moths."

Next comes the left of the volume, leading off with a brief description of morphology and how to identify the moth families. There are 85 families in Australia, out of some 140 globally. Some 69 families are treated, the missing ones being rarely seen and mostly tiny. The families are arranged from primitive to the highly derived, starting with the Micropterigidae and ending with the Noctuidae. The distinguishing characters of each family are given, having been chosen to be observable with a magnifier. All specimens are shown in color, alive in a natural setting with the images truly beautiful. The write-ups cover the important biological features of each family with number of known species in the fauna and globally cited. There are 13 brief "boxes" expanding on remarkable stories in selected groups, as the Bogong moth (an aboriginal food but with other features related to its abundance), witjubi grub (delicious), and pollination (remember the bees are disappearing).

You don't need to live in Australia to appreciate the book. But for the naturalist one surely wants to go and see some of the animals' figures and discussed. Although the work is not a scientific treatise, I not only hope that more works of this caliber are forthcoming for other regions, but that many, many more works of the kind can be generated for all groups of living things. And that finally public awareness can begin to focus on the vast diversity that very few humans seem to see. Before we loose it with either a whimper or a bang.

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**EDITORIAL**

Change is a feature of living systems at all levels, including publishing scientific journals about butterflies and moths. We first changed our format only four volumes ago from the beginning small size format. And here we are again, with new layout. Since our beginning nearly fifty years ago there has also been a revolution in production from cast type and letterpress to electronic production with inexpensive very high quality lithography and finally web based publication. We hope our readers like the new JRL.

There have been other changes, the most challenging now being the drastic economic scene worldwide that will touch everyone. The situation will not be kind in allowing us to pursue our interests. Many hard copy publishing venues may vanish along with the prior illusion of ever expanding prosperity for ever more people. Resources for study, both public and private will also suffer, and likely for a long time. We hope, however, this new environment will provide time for reflection and a re-growth of natural history study across all fields of biology everywhere. We view this neglect as deplorable given the projected changes that will doubtless occur, not to dwell on what is happening before our eyes.

We continue to believe that the JRL can provide a platform for good scholarly work. And we have the capability to publish this work in a timely manner. The problems with business, i. e. the billing, accounting, mailing lists, distribution of back issues, etc. should be behind us with Bioquip Products now handling all business aspects. There will be errors along the way, but feel free to contact Bioquip (Celia Whitman <celia@bioquip.com>) with a cc to Nancy Vannucci <jrl\_Lepidoptera@yahoo.com> and they will be corrected.

As for the Journal itself, we plan on two volumes per year, which will be billed as one unit. However, as any industry which cannot make products if they do not have raw materials, we cannot publish without manuscripts. With Nancy Vannucci as a full time employee, an excellent press in Los Angeles, and Bioquip for business support, our days of delay are past. A new editor is on the agenda as well, but I will struggle in the meantime. We urge your sending us your papers and remind you we have no page charges. All past journals (excepting the recent catalogue, Vol. 40) are on line. We are presently working on our own website to make these more available in addition to providing information about our other programs.

One other program, which seems unique, is our grants to students program. We can provide up to \$10,000 per year for this purpose, as maximum \$1000 grants. These are available to graduate students working in Lepidoptera research in less advantaged countries. With the current economic situation we take this to now be anywhere. The board of directors may shift direction, but we should have these funds comfortably available well into the future. At present our evaluation committee is working on eight submissions that will be announced shortly. The 2009 program will be announced shortly.

Finally, the LRF has joined in supporting the "Fundación Lepidóptera de Argentina" to develop an international exhibit featuring our favorite organisms as metaphors for conservation biology in conjunction with commissioned works by leading contemporary artists. Stay tuned.

We have the goal of expanding horizons in our field in as many imaginative ways as possible. These efforts not only include publication and encouragement of student programs, but public outreach. The latter is difficult as mass entertainments divert awareness of natural history biology and conservation in the public eye. We intend to keep trying and trust that you will support the Foundation in continuing these efforts. We thank you in advance. Please feel free to contact us at any time with suggestions and criticisms.

Rudi Mattoni, editor



## INSTRUCTIONS TO AUTHORS

**SUBMISSION OF MANUSCRIPTS.** Papers must be written in English. Your initial manuscript must be submitted as an electronic version by e-mail to the editor, preferably as a WORD document, double-spaced. **Do not format the text and do not justify the right margin.** Use only the regular and italic fonts, with the italic font only for the scientific names of the genus and species. Do not use boldface or vary type size (12 point preferred) for any sections or headers. Put returns only at the end of paragraphs, not at the end of each line. Use one tab to indent each paragraph. At the time of initial submission, all images (black and white or color) should be sent in digital form, preferably in medium-high quality JPEG format.

Upon acceptance of a paper, higher quality images will be requested. Files may be submitted by e-mail, or CD. At this stage digital images should be TIFF, or maximum quality JPEG files with at least 2700 x 4000 pixels resolution. Should you have further queries on this subject, please contact the technical editor.

**TITLE MATERIAL.** All papers must include complete title, author's name(s), institution(s), and address for correspondence, including e-mail address. A family citation must be given in parentheses (Lepidoptera: Hesperiiidae) for referencing.

**ABSTRACT.** Max. 300 words. No citations or figure references.

**KEY WORDS.** Max. 10 words in addition to those in the title.

**TEXT.** The text of a regular research paper should be clearly structured: e.g. introduction, material and methods, results, discussion, etc. with acknowledgements and literature cited at the end. Papers to be considered as Notes, Opinion pieces, or Book Reviews need not follow this structure. A note with four or fewer references should have these cited in the body of the text.

**NAME CITATIONS AND SYSTEMATIC WORKS.** The first mention of any organism should include the full scientific name with unabbreviated name of author(s) and year of description. Taxonomic descriptions must comply with the rules of the ICZN (4th edition).

**TABLES.** Present tables in the simplest form possible. Tables must be numbered serially with Arabic numerals independent from illustrations. Tables should be provided at the end of the paper on separate pages and not embedded in the body of the text. Put the legends for tables on a separate page. Tables should not repeat information that is already given in the text of illustrations. When formulating tables, keep in mind that the final table will fill 1 column (width 8 cm or 2 columns (16,5 cm).

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Atkins, A. F. 1975. The life history of *Anisynta tillyardi* Waterhouse and Lyell (Lepidoptera:Hesperiiidae: Trapezitinae). Australian Entomological Magazine 2: 72-75.

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## IN THIS ISSUE

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## PAPERS

- The life history of *Hypanartia dione dione* (Lepidoptera: Nymphalidae) in northeastern Ecuador  
*Havold E. Greeney and Carina Chicaiza Aguirre* 1
- Updated phylogeny, taxonomy, and diversification of *Janthecla* Robbins & Venables (Lycaenidae: Theclinae: Eumacini)  
*Robert K. Robbins and Robert C. Busby* 5
- $\delta^{15}\text{N}$  analyses of butterfly wings and bodies suggest minimal nitrogen absorption in carrion and dung puddling butterflies (Lepidoptera: Nymphalidae)  
*Freerk Molleman and Jeremy Midgley* 14
- Cost-effectiveness of Philippine butterfly species used in live exhibits: an assessment of longevity, encounter rate and behaviour.  
*Laura J. Robson, Adrienne Brewster and Gard Otis* 17
- The Neo-Riparian butterfly fauna of western Argentina  
*Arthur M. Shapiro* 24
- Revisiting the pre-European butterfly fauna of the Sacramento Valley, California  
*Arthur M. Shapiro* 31
- Population biology of *Euptoieta hegesia* (Nymphalidae: Heliconiinae: Argynnini) in an urban area in Southeastern Brazil  
*Julia Losada Tourinho and André Victor Lucci Freitas* 40
- Observations of overwintering nymphalid butterflies in underground shelters in SW and W Bohemia (Czech Republic) (Lepidoptera: Nymphalidae: Nymphalini)  
*Libor Dvořák, Joseph Belček and Zdeněk Fric* 45
- A revised classification scheme for larval hesperiid shelters, with comments on shelter diversity in the Pyrginae  
*Havold E. Greeney* 53
- Preliminary field survey of butterflies on Xishan Hill (Kunming, Yunnan Province, China)  
*Hu Shaoji* 60
- A newly observed form of symbiotic relationship between Reverdin's blue *Lycoides argyrognomon praeterinsularis* (Verity), (Lycaenidae) and *Camponotus japonicus* Mayr (Formicidae)  
*Michihito Watanabe and Yasuo Hagiwara* 70

## NOTES

- Fabaceae, a new host plant family for *Hypanartia* and for the Neotropical Nymphalinae (Lepidoptera: Nymphalidae)  
*Lucas A. Kaminski and André V. L. Freitas* 76
- Duration of molt in a Neotropical butterfly (Lepidoptera: Nymphalidae)  
*Felipe A. P. L. Costa* 77
- Euselasia mys* larva (Stichel, 1919) (Lepidoptera: Riodinidae) a potential pest on *Eucalyptus* in Brazil?  
*Marcus A. Soares, Teresinha V. Zanuncio, José C. Zanuncio, Olaf H. H. Mielke and José E. Seirão* 80
- Observations of late instar larva survival of *Cotesia* (Hymenoptera: Braconidae) parasitoid attack of *Euphydryas anicia cloudcrofti* (Lepidoptera: Nymphalidae)  
*Rachael E. Ryan and Brook Milligan* 82

## BOOK REVIEWS

- Olethreutine moths of Australia (Lepidoptera: Tortricidae) by Marianne Horak, with contributions by Furumi Komai, 2006  
*Joaquín Baixeras* 84
- A guide to Australian moths by Paul Zborowski and Ted Edwards, 2007  
*Rudi Mattoni* 85

## EDITORIAL

- Rudi Mattoni* 87